Ecology of Rays on Tropical Coral Reefs

Thesis submitted by
Carolyn Samantha Sherman
Bsc.Hons (University of Guelph, Guelph, Ontario)
MSc. (James Cook University, Townsville, Queensland)
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- Philippines
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ABSTRACT

Rays are a diverse group of elasmobranchs in both their morphology and ecology. They are among the most threatened elasmobranchs according to the International Union for the Conservation of Nature (IUCN), however, little is known about their life history, behaviour or population status. To be able to improve management of declining ray populations, their distribution and ecology must be better understood. Coastal species are most at risk from anthropogenic effects, however, the extent of impacts on rays have not been widely documented. Rays serve important ecosystems functions including stabilizing food webs and acting as ecosystem engineers through bioturbation. As mesopredators, rays prey on a variety of primary consumers, while also being prey for apex predators. Because of the many linkages in food webs among apex predators to producers, food web stabilization by mesopredators prevents trophic cascades. Some rays also serve their ecosystems through bioturbation, the biological reworking of sediments. During the act of feeding, some rays create feeding pits which oxygenate sediments, provides habitat for small teleosts and crustaceans, and facilitates meiofaunal movement. While rays serve important roles in their ecosystems, there is little species-specific information available. The lack of research is partially due to the cryptic nature of rays, making them difficult to study, and partially due to the charismatic nature of their relatives the sharks, which have received much more attention. Therefore, more research is needed to address the deficits in our knowledge of ray ecology and distribution.

Baited remote underwater video systems (BRUVS) are increasingly used to study fish communities, biomass, and animal behaviour. BRUVS entail deploying baited video cameras in the absence of human presence in order to survey fish and invertebrate populations. This

methodology reduces human influence on the study species and encourages more natural behaviours than with human presence. Due to the popularity of BRUVS approaches, there are many analysis methods. MaxN, which refers to the maximum number of individuals observed of a species in a single frame of a video, is the most commonly used metric of relative abundance when analysing BRUVS data. Chapter 3 presents a novel metric for BRUVS analysis that involves identifying and counting distinct individuals (MaxIND) to quantify the accuracy of MaxN. Individual oriental bluespotted maskray (*Neotrygon orientalis*) and the bluespotted fantail ray (*Taeniura lymma*) were identified on BRUVS by spot patterns, tail characteristics, and sex at three sites in Malaysian Borneo. We demonstrated that MaxIND gave abundances that were 2.4 and 1.1 times higher than MaxN for *N. orientalis* and *T. lymma*, respectively. These differences between methods were consistent for each species between sites regardless of the presence of marine reserves.

However, differences in abundance estimates from MaxN to MaxIND were apparent between species, indicating that correction factors need to be developed on a species basis to better estimate true abundance. While identifying individuals is time consuming, it provides improved accuracy and information about populations. We therefore recommend the use of MaxIND when rare and threatened species are present, in high density populations, and for behavioural analyses, where distinguishing features are present.

Ecological sampling must yield consistent results in order to reliably quantify predator populations. BRUVS are increasingly being used to evaluate and monitor predator communities in marine ecosystems. Many BRUVS studies compare multiple coral reef sites sampled at a single point in time. As coral reef monitoring using BRUVS grows in its capacity to provide data relevant to sustainable management, marine protected area efficacy, and

overall reef health, understanding repeatability of sampling results is vital. Chapter 4 examined the repeatability of BRUVS results for the elasmobranch community both within and between seasons (dry and wet) and years, and explored environmental factors affecting abundances at two sites in Bau Bau, Indonesia. A total of 1139 elasmobranchs (69% rays, 31% sharks) were observed on 956 BRUVS across six sampling events. Consistent results were found both in species composition and abundances within a season and across multiple years using the same sampling protocol (number and location of BRUVS). However, abundances of all sharks and rays were significantly higher in the wet season in both years. The elasmobranch community was significantly different between the two sites sampled in a consistent manner. The results demonstrated that while BRUVS are a consistent, reliable and repeatable method for surveying elasmobranchs, care must be taken in timing of sampling various regions to ensure accuracy when comparing multiple locations as season was an important factor in the results.

Coral reef ecosystems are highly dynamic environments with complex trophic interactions and environmental drivers. Rays are important members of these systems, however, in areas like Southeast Asia they are often heavily fished. Their conservation is difficult, as many countries in which they are fished do not have the capacity for effective fisheries management. For chapter 5, BRUVS were deployed at 70 reefs in 11 countries across the Coral Triangle and Australasian regions to determine ray abundances and assemblage. In 3426 BRUVS deployments, 1069 ray individuals were observed. The three most abundance species / genera were maskrays (*Neotrygon* spp.), fantail rays (*Taeniura* spp.), and eagle rays (Generas: *Aetobatus, Aetomylaeus, Myliobatus*). Ray assemblage was relatively consistant across the study area, however, ray abundances varied greatly with only a single individual in Vietnam to a very high abundance of rays in Indonesia. The differences in

abundances are likely a reflection of fishing pressure and fisheries management. In countries with low fishing pressure, communities were species rich in both rays and sharks. Countries with moderate fishing pressure began to lose species richness, especially of sharks, although abundances of rays remained similar. With high fishing pressure, only small productive species of rays were present, and these were abundant due to the lack of top predators (i.e. sharks). Finally, in countries with extremely high fishing pressure, even productive species were absent. In order to conserve rays and their ecosystem services, fisheries management must be addressed. In some cases this requires fisheries management implementation and in some cases may involve increased management efficacy. Additionally, habitat quality and characteristics also affect the ray community at finer scales than fishing pressure. Benthic relief was most important to all rays with some species preferring low relief areas and some preferring high relief (coral dominated) areas. Thus, in addition to fisheries management, habitat quality and conservation is also important for ray species.

Sharks are decreasing in abundance in many coral reef habitats, but the ecosystem effects of this loss are poorly understood. Rays are a prevalent mesopredator in tropical coral reef ecosystems experiencing low fishing pressure that are preyed upon by top predators like sharks. Across Southeast Asia and the Western Pacific there are varying abundances of coral reef predators that consume rays. Studies have suggested reduced predator abundances leads to increases in mesopredator abundance (mesopredator release) and potentially trophic cascades. In this study, we examined the relationship between top predator abundance (sharks) and the abundance and behaviour of two genera of small benthic rays using BRUVS at 19 sites across six countries. Where predators were more abundant, the bluespotted maskray complex (*Neotrygon* spp.) and two species of fantail rays (*Taeniura*

lymma and *T. lessoni*) were sighted less often, possibly because of lower abundances. However, small ray behaviour was significantly affected by predator abundance. Individuals of focal ray species visited BRUVS significantly fewer times at sites with higher predator abundances. Where predators were less abundant, rays spent significantly more time in the video frame, visited BRUVS more often, and were more likely to feed from bait bags. In addition to predator abundance, small ray presence was significantly influenced by relief and depth. *Neotrygon* spp. were more abundant on deeper, lower relief habitats, while *Taeniura* spp. were more prevalent in reef-associated shallow, high relief habitats. Overall, this chapter found that predator abundance had a significant effect on small benthic ray abundance and behaviour in the presence of BRUVS. The results demonstrate that changes in behaviour associated with the loss of predators may make the interpretation of phenomena like mesopredator release more challenging unless behavioural effects are taken into account.

This thesis demonstrates the many uses of BRUVS as a tool for surveying ray abundances, behaviours, and assemblage. A variety of analysis techniques were used for BRUVS data, with results proving the effectiveness of this survey method. Using the newly described metric MaxIND, more accurate abundance estimates and behavioural analyses are able to be performed in a natural setting. As there is limited data about rays on coral reefs globally, this thesis provides basic information about ray assemblages and abundances across the Coral Triangle and Australasian regions. Countries within these regions have extremely variable fishing pressure and management capacity leading towards changes in ray populations. In order to conserve ray species, improved fisheries management and habitat preservation are needed.

Chapter 1

General Introduction

Plate 1. Liberty waits at Pentai Kecil on Pulau Siompu in Bau Bau, Indonesia (July 2019).

Elasmobranchs inhabit every ocean on earth. There are over 1200 described species, over half of which are rays (Naylor et al. 2012; White et al. 2015). Rays, (elasmobranchs with ventrally located gill slits) that are generally dorsoventrally flattened, are a diverse group including species with pelagic, epipelagic, and demersal habits (Compagno 1990). Most species are demersal, with few exhibiting pelagic lifestyles (Last et al. 2010). Demersal rays demonstrate the greatest morphological and behavioural diversity, and include skates (Families: Rajidae, Anacanthobatidae, and Arhynchobatidae) that usually inhabit the deep-sea, as well as stingrays (Family: Dasyatidae) and shark-like rays (Families: Pristisdae, Rhinidae, Rhinobatidae, and Rhynchobatidae) that mostly occur in continental shelf waters (Last and Stevens 2009). Pelagic species (Families: Mobulidae, Myliobatidae, and Rhinopteridae) tend to be larger, with wing-like pectoral fins that are used for oscillatory swimming through open water (Rosenberger 2001; Forselledo et al. 2008). Rays also have varied diets that include polychaete worms, crustaceans, teleosts, and cephalopods, and trophic positions that range from 3.1 to 4.3, indicating they act as high level mesopredators (Jacobsen and Bennett 2013; Navia et al. 2017). The diverse characteristics of rays, including trophic roles, occupied depths, and diet mean they may occupy a variety of niches in different ecosystems, although their detailed role within these ecosystems is poorly understood (Suchanek and Colin 1986; Ajemian and Powers 2013).

Rays are among some of the most endangered of the elasmobranchs, however, little is known about their life history and behaviour patterns (White and Kyne 2010). The limited information available suggests that ~20% of rays are threatened by elevated risk of extinction as assessed by the IUCN (i.e. classified as Vulnerable, Endangered or Critically Endangered), and 25% are classified as ‘data deficient,’ both the highest proportions among elasmobranchs (Dulvy et al. 2014). The biggest threat to ray populations is fishing, both

through targeted fishing and as bycatch (Stevens et al. 2000). Like other elasmobranchs, rays are susceptible to overfishing due to their life history characteristics including low fecundity, large body size, long life span, and small litter size (Simpfendorfer and Wetherbee 2015). Rays are caught in many fisheries as bycatch, although catches have been decreasing in some locations over time as a result of population declines (Graham et al. 2001; Davidson et al. 2016).

Rays are caught in fisheries globally and in some locations are taken in higher abundances than sharks (Bonfil 1994). Southeast Asia is both a global biodiversity hotspot for elasmobranchs and the region with the highest catch of rays (White and Dharmadi 2007; Tittensor et al. 2010). The majority (77% by weight) of elasmobranchs landed in Chennai, India are rays (Mohanraj et al. 2009). Although a diverse group of species occur in the Pacific (Last et al. 2016), a thorough literature search has shown there have been few studies focused on rays in the region. In Southeast Asia, demersal rays are targeted for their commercial value (meat, skins) and importance to locals for subsistence (White and Dharmadi 2007; Lim et al. 2014). Shark-like rays are also caught and used as part of the fin trade (Clarke et al. 2006), while sawfishes (Family: Pristidae) are exploited for their rostra as well as fins and meat (Whitty et al. 2014; Dulvy et al. 2016). In addition to demersal rays, Mobulids are increasingly being targeted for their gill plates, which are dried and used as traditional medicines (Lawson et al. 2016). Rays also play culturally significant roles for Indigenous communities (Chin 2005). Recent population declines (Dulvy et al. 2014) mean that it is important to ensure conservation efforts include rays given their important social and cultural values, as well as their essential and diverse ecological roles (O'Shea et al. 2012b; Ajemian and Powers 2013), although overall previous conservation efforts have been solely focused on sharks.

Surveying rays has proven to be difficult due to their cryptic nature and wariness of humans (O'Shea et al. 2012a). Fishing and visual surveys performed by divers are some of the most commonly used methods to estimate ray populations and changes in abundances (Walker and Hislop 1998; Graham et al. 2001; Hoisington and Lowe 2005; Le Port et al. 2012). In some locations, market surveys have been used to determine local diversity and abundance (Clarke 2004; White et al. 2014). Fisheries sampling bias, gear selectivity and data limitations mean that catch data and market surveys may not representatively sample ray diversity. However, emerging methodologies such as fishery-independent Baited Remote Underwater Video Systems (BRUVS) can overcome some of these issues, and are also a non-lethal means for sampling rays (Cappo et al. 2004; White et al. 2013a). Baited remote underwater video systems are increasingly being used as a non-invasive method of surveying fish populations (Cappo et al. 2001; Harvey et al. 2013; Espinoza et al. 2014; Whitmarsh et al. 2016). The benefits of BRUVS include gathering a large amount of data from each deployment (habitat, fish community, predator abundance, etc.) without impacting the habitat (Cappo et al. 2001). BRUVS do require clear water to make observations (at least 1m visibility at the benthos), making them difficult to use in turbid areas (White et al. 2013a). Unlike unbaited videos, BRUVS have been established as a robust method of measuring abundance of the elasmobranch community in different habitats (Bernard and Götz 2012). Elasmobranch communities have been surveyed both directly and as part of the broader fish community using BRUVS in many regions including South Africa (De Vos et al. 2015), Australia (White et al. 2013a; Espinoza et al. 2014), Pacific USA (Papastamatiou et al. 2018), and others. Additionally, BRUVS have been used to show differences in relative abundance of reef sharks in areas with different protection statuses (Bond et al. 2012; Espinoza et al. 2014).

Marine protected areas (MPAs) have long been established as a tool for recovery of both corals and fish in coral reef ecosystems (Christie et al. 2002; White et al. 2002). The use of MPAs has increased in developing countries in recent years using both traditional (government) and non-traditional (community-based) management methods (Marinesque et al. 2012; Leenhardt et al. 2013; Sario 2016). Marine protected areas may also protect large predators like sharks (Robbins et al. 2006; McCook et al. 2010). Closures are predicted to have a positive effect on rays as well. For example, based on modelling of the Thornback ray (*Raja clavata*) in the Thames estuary, a three-season closure would reduce fishing mortality and enable population recovery (Wiegand et al. 2011). However, in field studies, this positive impact on rays has not been found yet (White et al. 2013a). BRUVS have been shown to be a useful tool in assessing positive impacts on relative abundance of predators in marine protected areas compared to those open to fishing (Bond et al. 2012; Beer 2015). An understanding of the effect of MPAs on ray diversity, abundance, and distribution is important because many developing countries are increasingly implementing marine protected areas and better management of existing ones (Langenheim 2016; McGuire 2016), and some Pacific countries have committed to establishing large MPAs as a targeted conservation policy (Chin et al. 2011). Better knowledge of current abundance, distribution, and movement of different ray species will provide a baseline for future work assessing the effectiveness of these newly introduced protected areas for rays.

The movement of sharks and rays on reefs is important because they provide energetic linkages between reefs and from reefs to coastal, pelagic and deep-water habitats (Couturier et al. 2013a; Heupel et al. 2015). Sharks are known to move between different reefs within the Great Barrier Reef Marine Park (GBRMP), (Heupel et al. 2010; White et al.

2013a; Espinoza et al. 2015), however, ray movements on coral reefs are poorly known (Davy et al. 2015). Many studies have looked at movement patterns of larger ray species on coral reefs, mainly manta rays (Dewar et al. 2008; Luiz Jr. et al. 2009; Germanov and Marshall 2014). Pelagic rays, like eagle rays, are known to make migrations between reefs (Ajemian and Powers, 2014). However, little is known about the drivers and extent of demersal ray movement in coral reef ecosystems. Additionally, few studies have examined the movement of demersal stingrays in locations without a tourism encounter program, which alters natural behaviours (Cartamil et al. 2003; Richards and Shivji 2005; Davy et al. 2015).

Coral reefs are facing extreme threats globally due to climate change, pollution, and overfishing (Spalding and Brown 2015; Wear 2016). Warming of the world's oceans due to climate change has created the longest and most intense bleaching event of corals (Heron et al. 2016). Coral loss from bleaching can significantly impact the structure and function of reef fish assemblages (Pratchett et al. 2018). In addition to coral bleaching, warming ocean temperatures increase cyclone frequency and intensity, which reduces the time coral reefs have to recuperate following a cyclone event (Cheal et al. 2017). The ability to recuperate is further inhibited by ocean acidification, which decreases calcification rates and increases the time needed for coral to rebuild their calcium carbonate skeletons (Hoegh-Guldberg et al. 2017). Corals are also at a greater threat to diseases due to plastic waste in reef ecosystems (Lamb et al. 2018). A reduction in coral cover can lead to lower fish species richness and abundances (Richardson et al. 2017). This reduction is amplified as coral reefs are being overfished globally (Zaneveld et al. 2016; Rogers et al. 2017). The many threats confronting coral reefs amplify the need for knowledge of coral reef associated species and their conservation.

Given the conservation status of rays and the pressure on coral reefs, the overarching purpose of this PhD thesis was to determine drivers of ray diversity, abundance and distribution throughout Southeast Asia and the western Pacific using BRUVS in both conventional and innovative ways. This was accomplished through four specific aims: 1) determine effectiveness of traditional BRUVS sampling methodology for coral reef rays, 2) investigate seasonal patterns in diversity and abundance of rays and how these affect repeatability of BRUVS sampling, 3) evaluate drivers of ray diversity, abundance and distribution through Southeast Asia and the Western Pacific, and 4) examine the relationship between ray abundance and shark abundance.

To accomplish these aims I reviewed the literature on the roles and movement patterns of rays on tropical coral reefs (Chapter 2). Chapter 3 examined the differences when estimating abundances of rays using a traditional BRUVS metric (MaxN) compared to a new metric (MaxIND). Chapter 4 examined repeatability of BRUVS results both within and between seasons and years through repeated sampling. Chapter 5 investigated the drivers of diversity, abundance, and distribution of rays on tropical coral reefs in Southeast Asia and the Western Pacific. Chapter 6 focused on ray behaviour and abundances in areas with varying predator abundances to investigate if there was evidence for mesopredator release on reefs with low predator abundance. Finally, Chapter 7 synthesized the data collected throughout this PhD thesis to understand the impacts of environmental and human activity on ray diversity, abundance, and distribution and how these may change with current fishing and management patterns.

Chapter 2

Functional Roles and Movement of Rays Within Marine Ecosystems

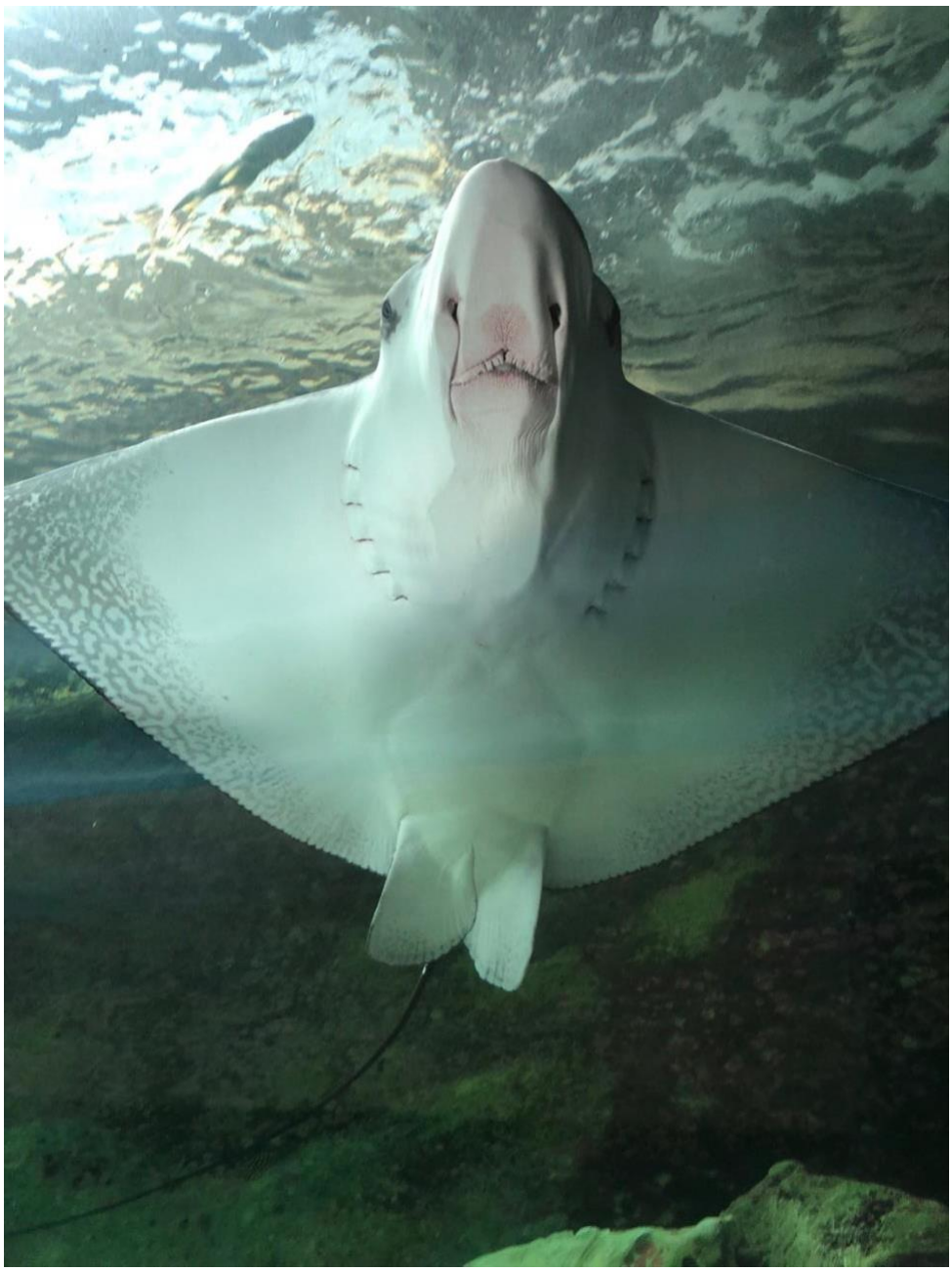

Plate 2. Eagle ray (*Aetobatus ocellatus*) at SEA LIFE Sydney Aquarium (August 2018).

2.1 Introduction

Elasmobranchs inhabit every ocean on earth. There are over 1200 described elasmobranch species globally, over half of which are rays (Naylor et al. 2012; White et al. 2015) including pelagic and demersal species (Compagno 1990). Demersal rays, in addition to being the most abundant, demonstrate the greatest morphological and behavioural diversity among rays (Last et al. 2010). Demersal rays include skates (Families: Rajidae, Arhynchobatidae, and Anacanthobatidae) that usually inhabit deep-sea habitats, as well as stingrays (Family: Dasyatidae) and shark-like rays (Families: Pristidae, Rhinidae, Rhinobatidae, and Rhynchobatidae) normally found in shallower waters of varying habitats (Ebert and Compagno 2007; Last and Stevens 2009). As their name suggests, pelagic rays (Families: Mobulidae and Myliobatidae) spend a majority of their time in the water column, however, they are also found in coral reef, deep-water, and estuarine habitats (Ajemian and Powers 2014; Thorrold et al. 2014; Braun et al. 2015). The diverse characteristics of rays reflect their occupancy of a wide variety of niches in different ecosystems, although their role within these ecosystems is not currently well understood. Rays are also an important food resource in many regions (Stobutzki et al. 2006) and play a cultural role in many communities (Chin 2005).

Rays are among some of the most endangered of the elasmobranchs (Dulvy et al. 2014), however, little is known about their life history and behaviour patterns (White and Kyne 2010). Despite limited information, 20% of rays are listed in a 'threatened' category by the IUCN and 25% are classified as Data Deficient (Dulvy et al 2014). In both cases these are the highest proportions among elasmobranchs (Dulvy et al. 2014). The biggest threat to ray populations is fishing, both through targeted fishing and as bycatch (Stevens et al. 2000).

Rays are susceptible to overfishing due to life history characteristics including low fecundity, large body size, long life span, and small litter size (White and Kyne 2010). They are harvested for their meat, skin, which is made into leather, and their fins for shark fin soup (Clarke et al. 2006; Das et al. 2007). Globally, rays are caught in higher abundances than sharks, contributing to their threatened status (Dulvy et al. 2014). As a result of population declines, ray catches have decreased in many locations (Walker and Heessen 1996; Graham et al. 2001; Ferretti et al. 2013).

Historically there has been limited research into ray life history and ecology. The majority of ray research has focused on a few species, particularly the two largest species in the genus *Mobula* (*M. alfredi* and *M. birostris*). While manta rays play important roles in their ecosystems, the diversity that occurs within rays requires studies of many different species.

In order to improve management of ray populations, their distribution and movement patterns must be better defined (Martin et al. 2007). No take marine protected areas (MPAs) have long been established as a tool for recovery of both corals and fish in coral reef ecosystems (Russ et al. 2015; Mellin et al. 2016). In order to understand the efficacy of no take MPAs for protecting rays, knowledge of their residence and movement patterns is required. Sharks are known to move between different reefs within the Great Barrier Reef Marine Park, (Heupel et al. 2010; White et al. 2013a; Espinoza et al. 2015), however, ray movements are poorly known (Davy et al. 2015). Seasonal closures are predicted to have a positive effect on some rays, based on modelling of the Thornback ray (*Raja clavata*) in the Thames estuary (Wiegand et al. 2011). However, in field studies, the impact of MPAs on rays is poorly understood

(White et al. 2013a).

Movement of individuals among habitats provides connectivity in the marine ecosystem through food web connections, parasites, and genetics (Verweij and Nagelkerken 2007; Richards et al. 2009). Many rays occur in reef ecosystems, including pelagic myliobatids and mobulids (Ward-Paige et al. 2013). However, demersal species are the most abundant and diverse group of reef dwelling rays (Last and Stevens 2009). Understanding ray movement patterns provides information about population and ecosystem connectivity, and the potential ecological roles mobile rays play in energy flows (Lundberg and Moberg 2003).

This review identifies current studies on ray movement and describes how far and often rays move within and between marine ecosystems and other key roles rays play within their ecosystems. It also identifies key knowledge gaps in current ray research.

2.2 Methods

This literature review examined publications found through searches using multiple databases (Zoological Record Plus, Web of Science, and Google Scholar) with the ray identifying keywords “batoid,*” or “ray,*” or “skate*,” or “guitarfish*,” or “wedgefish*” or “sawfish*” and each of: “movement,” “telemetry,” “photo ID” or “photo identification,” “home range,” “tag” or “satellite tag,” “stable isotope,” “laser ablation,” and “mark recapture.” Literature regarding freshwater stingrays (Potamotrygonids) was not included. Once papers were amassed from searches, references were combed to identify more movement studies.

For other sections of this review, similar batoid identifying keywords were used in the same databases as above to identify papers that may be of interest. In addition to the

ray identifying keywords, “bioturbation,” “feeding,” “diet,” “mesopredators,” and “feeding pit*” were searched. Additional publications were identified from the bibliographies of search results.

2.3 Ray Movement Patterns

Differences in ray propulsion modes have a direct effect on how efficiently and far they are able to travel. Pelagic and epipelagic rays, including myliobatids and the pelagic stingray (*Pteroplatytrygon violacea*), generally use their wing-like pectoral fins to oscillate

through open water (Forselledo et al. 2008). Their large ‘wings’ enable them to travel long distances at high speeds (Moored et al. 2008). Satellite tracking has showed individual oceanic manta rays (*Mobula birostris*) moving up to 1,151 km within 27 days, cruising with an average speed of 1.2 km/h (Graham et al. 2012). Benthic rays use a range of propulsion methods including punting, undulation, and oscillation (Macesic and Kajiura 2010; Dewey et al. 2012). Skates (Family: Rajidae) move along the benthos by punting, which is using their pelvic fins to propel themselves forward (Macesic and Kajiura 2010). Punting is an effective propulsion style enabling rapid movement and provides an additional propulsion method to flapping. Some dasyatid species are capable of moving through ‘augmented punting’ where they mainly use pelvic fins, supplemented with pectoral fin movement. These individuals are not able to move as fast or as far as true punters while using this type of propulsion (Macesic and Kajiura 2010). Other benthic species, like the bluespotted fantailed ray (*Taeniura lymma*), use undulation of the pectoral fins to propel themselves (Rosenberger and Westneat 1999). Shark-like rays move similar to sharks, using their caudal fin, however they generally move along the benthos (Rosenberger 2001). They are capable of moving at fast speeds

of at least 6.6 km/h and long distances, with one smalltooth sawfish (*Pristis pectinata*) moving 285 km in 59 days (Gutteridge et al. 2015) possibly within a strong current system. Propulsion method is not indicative of space use, as within each propulsion method, some species move further and faster than others. Different propulsion methods enable varied speeds of movement, however, other factors also play a role in movement distance and speed, including home range size and environmental factors (Farrugia et al. 2011).

Ray movement has been studied using a variety of methods including: acoustic telemetry (Corcoran et al. 2013), direct observation (Smith and Merriner 1987), pop-up archival tags (Le Port et al. 2008), mark recapture (Lowe et al. 2007), photo identification (Deakos et al. 2011), satellite tags (Ajemian and Powers 2014), sonar (McCauley et al. 2014), stable isotope analysis (Hussey et al. 2012) and genetics (Ovenden 2013). A variety of methods are necessary to study short-term and long-term movement of species, in addition to studying distances travelled.

Movement comprises a variety of different actions including habitat use, daily activity space, residency, and migration, among others. 'Habitat use' refers to the areas which individuals or species' use resources from throughout their lives, rather than travel through (Hammerschlag et al. 2011). An individual's 'space use' refers to the area of space that they occupy during a set period (daily, monthly, etc.)(Simpfendorfer et al. 2012). Different forms of migration include a relocation of a longer duration and larger scale than daily movements ('migration'), a repeated seasonal movement to better conditions ('seasonal migration'), and/or redistribution of a spatially extended population ('emigration')(Dingle and Drake 2007). 'Residency,' the opposite of migration, indicates that an individual is present in a given area for multiple days to years.

A total of 55 publications were found that studied ray movement comprising 30 different species (**Table 2.1**). The earliest publication was published in 1984, however, most studies were published in the past 10 years (**Fig. 2.1**). Most studies to date have focused on the two manta species (over 45% of the literature). Acoustic telemetry was the most commonly applied method to study ray movement, being used in 50% of published studies (**Fig. 2.2**). Ray movement was examined for periods of hours up to years, depending on the methodology used. Studies using manual acoustic telemetry tracked individuals for up to a few days with fine-scale precision (Klimley et al. 2005), whereas photo identification studies were able to show individuals resident over a 5-year span (Deakos 2012).

Rays showed large variations in speed, space use, and seasonality. Space use in rays varies dramatically across species, for example, the brown stingray (*Dasyatis lata*) was documented to use under 1 km^2, while the flapper skate (*Dipturus cf. intermedia*), has been documented to use spaces of over 17,000 km^2 in under 6 months (Cartamil et al. 2003; Pinto et al. 2016). Some rays were resident over the entire year, like the pink whipray (*Himantura fai*) in French Polynesia, where at least half of the tagged individuals were present for the entire 340 day study (Gaspar et al. 2008). Other rays undergo seasonal migrations, like the round stingray (*Urobatus halleri*), which is abundant in the Anaheim Bay Estuary in California during summer months and absent during the winter months (Jirik and Lowe 2012).

2.3.1 Migration

Migration occurs in many species for various reasons including food availability, thermal tolerance, and reproduction (Fryxell and Sinclair 1988; Dingle 1991; Witteveen et al. 2009). Understanding migration patterns is important, as rays will only have direct impacts on a given ecosystem during a period of residency. *Mobula*, the genus that includes the largest rays, are known to undertake seasonal migrations to follow blooms of plankton, their primary food source (Luiz Jr. et al. 2009; Anderson et al. 2011a). The oceanic manta, the larger species, tends to make longer migrations and has been shown to move repeatedly around the Yucatan Peninsula up to 1,151 km in just 27 days (Graham et al. 2012), whereas reef manta tend to stay in warmer waters, for example, travelling a repeated distance of ~500 km between Lady Elliot Island and Byron Bay in Queensland, found through photo ID (Couturier et al. 2011). Chilean devil rays (*Mobula tarapacana*), a close relative to mantas, have been tracked using pop-up archival tags moving up to 3,800 km at a speed of up to 50 km per day from August through January (Thorrold et al. 2014). Cownose rays (*Rhinoptera bonasus*) make shorter migrations than mantas and mobulas, for example, moving in and out of Mobile Bay, Mississippi. During periods outside of the bay, the rays spend a majority of their time inshore, moving an average of 9.5 km per day (Ajemian and Powers 2014). Other migratory species, like the thornback ray may only make short seasonal migrations, spending time in the Thames Estuary, England in spring and moving to deeper waters just outside the estuary in autumn (Hunter et al. 2006). The furthest recapture of a thornback ray was 276 km from the point of release, and 96% of recaptures occurred within the estuary (Hunter et al. 2006). Some demersal species in temperate waters exhibit seasonal movement possibly as a means of behavioural thermoregulation, like the thornback ray which moves into

the warm waters of the Thames Estuary in spring, and the round stingray, which were only present in a California estuary during warm summer months (Hunter et al. 2005; Vaudo and Lowe 2006; Jirik and Lowe 2012). There are still many unknowns in ray migration, particularly for smaller bodied and demersal species.

Studies of pelagic species generally show a migratory lifestyle, however, they can be resident and have large impacts in a localized area. Most pelagic species rely on benthic resources, with few exceptions including the pelagic stingray which consumes pelagic prey (Véras et al. 2009). Mantas, which are known to feed near the surface, have been found to also consume benthic deep-water zooplankton through stable isotope analyses and pop-up archival tags (Couturier et al. 2013a; Braun et al. 2014). Within pelagic species, some populations are considered migratory, while others remain resident. Spotted eagle rays (*Aetobatus narinari*), for example, are considered migratory, although separate populations may exhibit different migratory patterns (Ajemian and Powers 2014; Sellas et al. 2015). In Bermuda, spotted eagle rays appear to be resident, making excursions to adjacent reef habitats for a few days at a time before returning inshore (Ajemian and Powers 2014). Habitat use of the eagle rays includes a variety of ecosystems, however, sandy areas adjacent to reefs, like inshore lagoons, are most important to them as this is their main feeding ground (Ajemian et al. 2012). Cownose rays in Florida make seasonal migrations, exhibiting periods of residency between migrations (Collins et al. 2007). While resident, their daily activity space varies by location, for example, in estuarine systems activity space is <20 km per day (Collins et al. 2008), while in coastal areas, individuals may move up to 50 km in a single day (Ajemian and Powers 2014). In both the cownose ray and spotted eagle ray, males moved greater daily distances than females (Collins et al. 2007; Ajemian and Powers

2014). Although migration often focuses on horizontal movement, some movement occurs vertically.

In addition to horizontal movements, some pelagic rays show vertical movements, diving to depths of up to 2,000 m (Thorrold et al. 2014). Diving behaviour is likely associated with foraging, as reef mantas have stable isotope signatures indicating deep-water zooplankton occur in their diet (Braun et al. 2014). Chilean devil rays exhibit diving behaviour during the day, enabling them to heat up in surface waters while the sun is up, before and after dives (Thorrold et al. 2014), whereas reef mantas perform their dives throughout the night, remaining near the surface during daylight hours (Braun et al. 2014). Other pelagic species, like the spine-tail devil ray (*Mobula japonica*), do not dive, but rely on the diel migration of their prey, feeding at night while prey are above 50 m depth (Croll et al. 2012). Each of these feeding strategies enables these pelagic rays to consume deep-water prey.

2.3.2 Residency

Some rays, mainly skates, occur in deep-water (Ebert and Compagno 2007). These species tend to be resident, with mark-recapture studies showing individuals recaptured within 150 km up to 20 years later (Templeman 1984; Walker et al. 1997; King and McFarlane 2010). On the west coast of Canada, over 75% of big skates (*Raja binoculata*) were recaptured within 20 km of their capture site up to five years post release (King and McFarlane 2010). This apparent small space use does not hold true for all skates, as satellite telemetry of the flapper skate has shown use of over 17,000 km^2 in less than a year (Pinto et al. 2016). Skates are the most speciose group within the ray order, however due to their occurrence in deep-water habitats, there is little information

about their movement (Ebert and Compagno 2007).

Although more accessible to researchers, there are still many unknowns in movement of shallow coastal ray populations. Estuaries and coastal waters may be important nursery grounds for elasmobranchs, including rays (Heupel et al. 2007; Dale et al. 2011). Nursery grounds are indicated by high abundances of young-of-the-year individuals that remain or return to the area for an extended period of time, and an area that is used from year to year for this purpose, thus making them important to identify (Heupel et al. 2007). In California, a majority of shovelnose guitarfish (*Rhinobatos productus*) captured within estuary grounds were juveniles and recaptures did not occur from one year to the next, indicating the possibility that this is a nursery for the species (Farrugia et al. 2011). In Western Australia, juveniles of three ray species were detected in a small, shallow area adjacent to a mangrove forest for up to 16 months, indicating this area as a possible nursery habitat for these species (Cerutti-Pereyra et al. 2014). Coastal ecosystems are facing increasing anthropogenic pressures, particularly near major human settlements (Halpern et al. 2008; Brodie and Waterhouse 2012). These are important ecosystems for many ray species, therefore, impacts from pressures must be better understood.

In addition to using estuarine and coastal ecosystems as nurseries, adult rays also use these habitats throughout their lives. In Cleveland Bay, Queensland, giant shovelnose rays use the bay for a portion of the year, leaving in December and returning in spring the following year (White et al. 2013b). While resident, space use of the rays is up to 64 km^2, for individuals with lower residency indexes and as low as 6 km^2 for individuals with high residency indices (White et al. 2013b). Other species, like the smalltooth sawfish, spend their time in shallow water (<4m deep) near mangroves for up to 99.9% of their

lives, only venturing to deeper water when moving between mangrove habitats (Gutteridge et al. 2015). Other rays, like the small-eyed ray (*Raja microcellata*) and the blonde ray (*Raja brachyura*) are found near coasts but exhibit no apparent residency to the bay in which they were captured when monitored over a 650 day period (Morel et al. 2013). It is unclear whether developments of coastal areas have already had an effect on ray populations and movement, however, increasing coastal development is expected to have negative effects on the adjacent marine ecosystem through habitat loss and increase in sedimentation.

2.3.3 Space Use

In addition to development, tourism and other resource use can affect the natural movement of rays (Nyström et al. 2000; Halpern et al. 2008). At Stingray City in the Cayman Islands, southern stingray movement was examined relative to provisioning and showed individuals that are fed were more active during daytime in a small space of 0.014 km^2, whereas wild individuals were more active at night over a significantly larger area of 0.63 km^2 (Corcoran et al. 2013). Similarly, in Moorea, pink whiprays arrived at one of two provisioning sites 1-2 hours prior to the arrival of people in anticipation of feeding indicating their movement is due to the presence of humans providing food at these sites (Gaspar et al. 2008). No studies have looked at the unfed population of pink whiprays in coral reef ecosystems. Studies of natural movements are required to better understand how human presence is affecting rays and changing their natural behaviour.

Few studies have examined natural ray movement in coral reef ecosystems. The limited information available suggests that movements vary widely between species and are affected by different variables. One study found Hawaiian stingrays (*Dasyatis lata*),

showed significant increases in space use at night, using up to 2.77 km^2 compared to under 0.15 km^2 during the day (Cartamil et al. 2003). Movement of the Hawaiian stingray was not influenced by tides (Cartamil et al. 2003), however, tide does play an important role in the movement of the mangrove whipray (*Himantura granulatus*)(Davy et al. 2015). Mangrove whiprays were observed to use mangrove habitats as refuge areas during high tide, often hiding within the prop roots. At low tide, rays moved to coral reef habitats as mangrove habitats dried (Davy et al. 2015). In the northern Gulf of Mexico to southern Brazil, genetics were used to show limited gene flow between populations of southern stingrays separated by just 120 km, indicating distinct populations and hence limited movements over these spatial scales (Richards and Shivji 2005). Because few studies have examined demersal rays in reef ecosystems, little is understood about their movement. Currently, whether or not these rays move between reefs or stay resident to a single reef is unknown, leaving many unanswered questions.

Ray movement patterns differ depending on species, size, location, and propulsion method (Rosenberger 2001; Klimley et al. 2005; Collins et al. 2007). There has been a heavy focus on migratory ray species and movement of resident species is not well understood. Demersal rays, particularly in coral reef ecosystems, require further research to better define movement, which will help refine their ecosystem roles. For migratory species that are of conservation concern, we must understand their movement patterns so they are afforded protection throughout their range (Heupel et al. 2015).

2.4 Functional Roles of Rays

2.4.1 Rays as Mesopredators

Prey species and feeding methods vary among rays, however, all species act as mesopredators within their respective food web (Opitz 1996; Ajemian and Powers 2014). Mesopredators occupy the trophic level between primary consumers and top predators providing important links in the food web (Prugh et al. 2009). Due to fishing, top predators are being removed from many marine ecosystems (Ferretti et al. 2010), which can lead to an increase, or shift in mesopredator abundance and reduction in primary consumers (Bascompte et al. 2005; Grubbs et al. 2016). This is a type of trophic cascade referred to as 'mesopredator release' (Rayner et al. 2007). The effects of mesopredator release may be
masked if mesopredators in the system are also fished (Ferretti et al. 2010). For example, in places like SE Asia where rays are heavily fished, the effects of a mesopredator release may not be apparent due to removals from the system (White and Kyne 2010).

Mesopredators within a system have varied diets to keep primary consumer populations down and avoid bottom-up trophic cascades. Rays range in their diets, with some consuming small soft-bodied invertebrates, molluscs, teleosts and even cephalopods (Sasko et al. 2006; Ajemian and Powers 2012; Lipej et al. 2013). The variety in diet of different types of ray mesopredators means their role within ecosystem food webs can differ significantly.

Mouth position provides some indication of feeding method. Demersal rays have ventral mouths, making it easier to excavate sediment and eat smaller benthic

organisms (Dean et al. 2007). Some pelagic rays, like myliobatids also have ventral mouths and feed on benthic prey, leading to a similar diet to that of many demersal rays (mainly invertebrates)(Sasko et al. 2006; Tilley et al. 2013a). Pelagic species from the family Mobulidae have terminal mouths and consume plankton while swimming in the water column (Couturier et al.
2013b). One of the exceptions to this pattern is another pelagic ray, the pelagic stingray, which has a ventrally located mouth but consumes larger pelagic prey like teleosts and cephalopods (Véras et al. 2009). This change in lifestyle enables the pelagic stingray to avoid competition for food with demersal rays and plankton-eating pelagic rays.

In ecosystems where resources are limited, several species of rays can co-occur, increasing competition for resources. Resource partitioning enables species within an ecosystem to coexist through their differing use of space, and other resources (Schoener 1974). In some instances where many predators (sharks) are present in the ecosystem, resource partitioning may not occur (Vaudo and Heithaus 2011). A large number of apex predators in the system can reduce local species abundance and diversity, and thus reduce competition for habitat and prey. For example, in Shark Bay, Western Australia, several species of demersal rays have highly overlapping habitat and food sources in an environment with high predator abundance (Vaudo and Heithaus 2011). In southern Brazil, where ray predators exist in lower abundances, the higher density of rays has led to similar ray species having different and highly specialised diets with minimal overlap (Bornatowski et al. 2014).
Therefore, the level of predation and competition may affect ray dietary profiles, specialisation, and niche separation.

2.4.2 Ray Bioturbation in Reef Ecosystems

Bioturbation is the movement of sediment by benthic biota (Meysman et al. 2006). Bioturbation is an essential process in soft bottom habitats as it increases nitrogen fixing, deepens the anoxic zone within sediments, and can provide habitat for small animals (Laverock et al. 2011; O'Shea et al. 2012b). Predominant bioturbators in many reef ecosystems include callianassid shrimp and burrowing invertebrates that continuously turn over upper layers of sediment such that the upper 5mm of an entire reef ecosystem could be turned over within a year (Uthicke 1999). In addition to invertebrates, many fish species also act as bioturbators during burrowing, escaping, and feeding behaviours with varying amounts of sediment movement (Suchanek and Colin 1986). Rays that forage in the benthos also act as important bioturbators in reef ecosystems (Thrush et al. 1991).

Through bioturbation, rays redistribute relatively large amounts of sediment during feeding events and while burying in the sand, disrupting the benthos to depths of up to 15 cm (Suchanek and Colin 1986). Rays that feed on benthic organisms create feeding pits during predation events, which is typically observed as an oval depression in the benthos (Grant 1983). The feeding pits cause disturbances in the sediment that vary in size and depth and may be revisited by an individual multiple times over several days (Reidenauer and Thistle 1981; O'Shea et al. 2012b). Revisits can either maintain the pit or increase the depth and size of the pit (O'Shea et al. 2012b). In temperate locations, feeding pit abundance is seasonal, with highs during the summer months and minimal to no pits observed in winter months, indicating a shift in feeding grounds (Hines et al. 1997; Cross and Curran 2004; Blanco-Parra et al. 2012). This behaviour has occurred for millions of years, as feeding pits have been found in Cretaceous sediments (Howard et

al. 1977). Although rays are not responsible for the same magnitude of sediment movement as burrowing organisms, their abrupt disturbances serve different functions to the ecosystem, as described below, than the constant bioturbation of burrowers (Thrush et al. 1991).

Feeding pits are used secondarily by other species once the ray has vacated the area. The pits can act as habitat for small fish, crabs, and other invertebrates (O'Shea et al. 2012b). Ray feeding pits are often found in intertidal sand flats, therefore, water remains within pits during low tide, providing refuge for small teleosts (O'Shea et al. 2012b). In addition to habitat, other species, like small fish and crustaceans, may exploit the pits to access normally buried prey items (Thrush et al. 1991). Without the presence of rays and their feeding pits, there may be less habitat for other organisms on reef flats.

Prey species are not the only organisms removed during feeding events. Meiofaunal abundances can be significantly reduced due to the immediate disturbance of sediment during a feeding event (Cross and Curran 2004). Meiofauna are usually able to recover within 24 hours (Reidenauer and Thistle 1981). Recovery includes individuals surfacing from deeper in the sediment layer and those that arrive through tidal movements (Reidenauer and Thistle 1981). Large disturbances in sediment from ray feeding activity facilitate meiofaunal immigration and emigration as well as postlarval dispersal, both of which may strengthen the population diversity (Thrush 1999). Facilitating immigration and emigration of meiofauna is one of the important ecosystem roles rays play.

Rays can also have perceived negative effects on the ecosystem through their feeding

activity. Cownose rays have been implicated in the significant decline of eelgrass beds in the Chesapeake Bay because their bioturbation uproots eelgrass (Orth 1975). Removal of eelgrass was followed by significant losses in invertebrate and teleost biomass. Rays are also able to disrupt growth of seagrasses with shallow roots and small rhizomes, changing the composition of seagrass beds to species with deeper roots and larger rhizomes (Valentine et al. 1994). In addition to biological changes, removal of a large proportion of the seagrass in the Chesapeake Bay led to beach erosion (Orth 1975). Through the single action of feeding, rays serve many ecological functions including: influencing the meiofaunal community, changing habitat structure, and oxygenating sediments.

2.5 Conclusions

Rays occupy diverse ecological niches although these niches are not currently well understood. Few studies have attempted to quantify ray movement. Existing data has shown large variations in both pelagic and demersal species' movement patterns as some species migrate long distances, while others remain resident to small spaces. Movement of demersal rays is not well understood, although they may play important roles in ecosystem connectivity. A high proportion of ray species are considered sedentary, however, current literature is heavily focused on migratory and highly mobile species, leaving a large knowledge gap. Within ecosystems, rays are an important part of the food web, providing food web stability as mesopredators, however, their diets may differ significantly in different locations. More species and site specific diet information is required to fully understand the role rays play in different food webs. Rays also act as ecosystem engineers, creating habitat through bioturbation, however, documentation of feeding pits is limited to tidal flats. Rays may

have effects on meiofauna and sediment oxygenation in other soft benthos habitats that are consistently underwater. Considering the diverse functions rays provide to their respective ecosystems, greater understanding of their overall ecology (trophic role, ecosystem services, movement patterns, etc.) is needed as well as more diverse species-specific ecology.

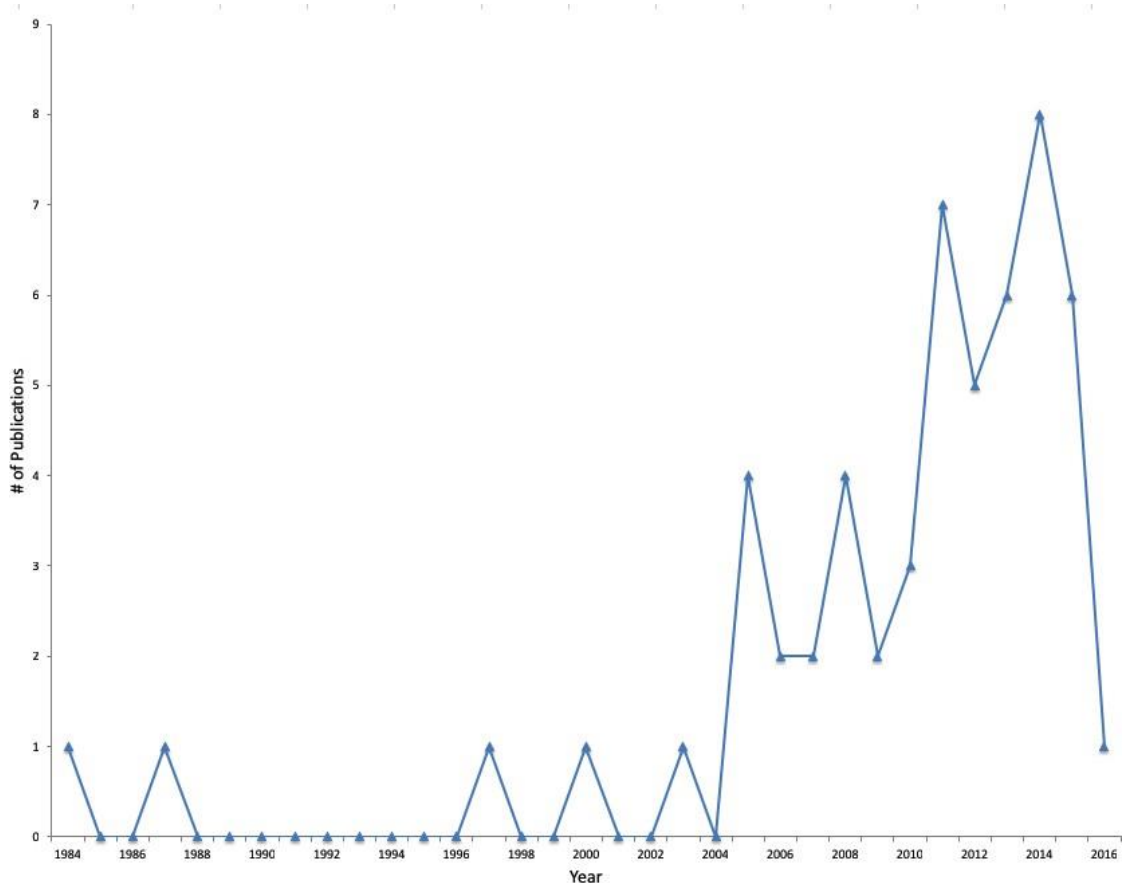

Figure 2.1. Number of publications per year on ray movement from 1984 to present. Most papers have been published after 2005.

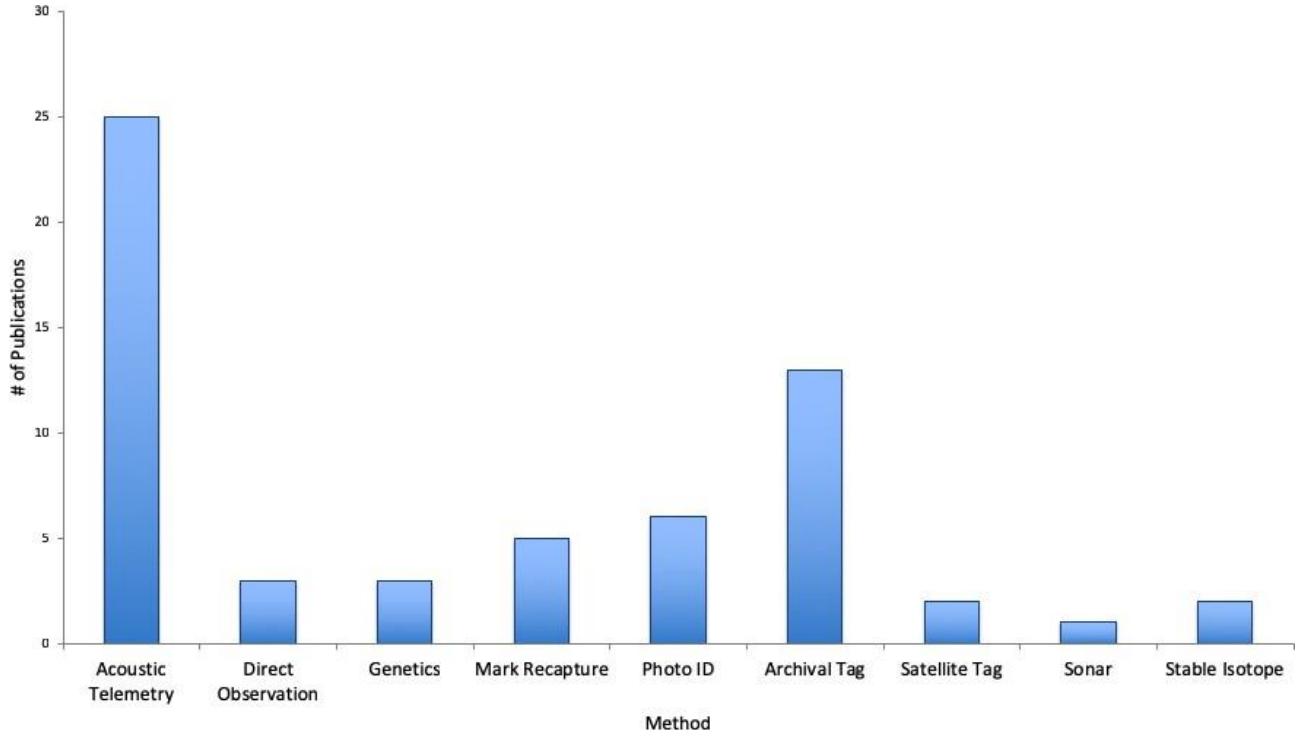

Figure 2.2. Publications studying ray movement using different methods. A total of 55 publications (some using multiple methods) were found from 1984-2016.

Table 2.1. Publications that discuss ray movement. Each row indicates a single publication that may include multiple methods or species.

Authors	Year	Method	Species
Templeman	1984	Mark Recapture	*Raja radiata*
Smith and Merriner	1987	Direct Observation	*Rhinoptera bonasus*
Walker et al.	1997	Mark Recapture	*Raja clavata* *Raja montagui* *Raja radiata*
Matern et al.	2000	Acoustic Telemetry	*Myliobatus californica*
Cartamil et al.	2003	Acoustic Telemetry	*Dasyatis lata*
Klimley et al.	2005	Acoustic Telemetry	*Myliobatus californica*
Hunter et al.	2005a	Archival Tag	*Raja clavata*
Hunter et al.	2005b	Archival Tag	*Raja clavata*
Richards and Shivji	2005	Genetics	*Dasyatis americana*
Vaudo and Lowe	2006	Acoustic Telemetry	*Urobatis halleri*
Hunter et al.	2006	Archival Tag	*Raja clavata*
Lowe et al.	2007	Mark Recapture	*Urobatis halleri*
Collins et al.	2007	Acoustic Telemetry	*Rhinoptera bonasus*
Le Port et al.	2008	Archival Tag	*Dasyatis brevicaudata*
Gaspar et al.	2008	Acoustic Telemetry	*Himantura fai*
Collins et al.	2008	Acoustic Telemetry	*Rhinoptera bonasus*
Dewar et al.	2008	Acoustic Telemetry	*Mobula birostris*
Whitty et al.	2009	Acoustic Telemetry	*Pristis microdon*
Richards et al.	2009	Genetics	*Aetobatus narinari*
King and McFarlane	2010	Mark Recapture	*Raja binoculata*
O'Shea et al.	2010	Direct Observation	*Mobula birostris*
Simpfendorfer et al.	2010	Acoustic Telemetry	*Pristis pectinata*
Vaudo	2011	Acoustic Telemetry	*Glaucostegus typus* *Himantura fai* *Himantura uarnak* *Pastinachus atrus*
Farrugia et al.	2011	Acoustic Telemetry	*Rhinobatos productus*
Couturier et al.	2011	Photo ID	*Mobula alfredi*
Anderson et al.	2011	Direct Observation	*Mobula alfredi*
Deakos et al.	2011	Photo ID	*Mobula alfredi*
Marshall et al.	2011	Photo ID	*Mobula alfredi*
Simpfendorfer et al.	2011	Acoustic Telemetry	*Pristis pectinata*
Jirik and Lowe	2012	Acoustic Telemetry	*Urobatis halleri*
Ajemian et al.	2012	Acoustic Telemetry	*Aetobatus narinari*
Deakos	2012	Photo ID	*Mobula alfredi*
Croll et al.	2012	Archival Tag	*Mobula japanica*
Graham et al.	2012	Satellite tag	*Mobula birostris*

Corcoran et al.	2013	Acoustic Telemetry Mark Recapture	*Dasyatis americana*
Carlson et al.	2013	Archival Tag	*Pristis pectinata*
Poulakis et al.	2013	Acoustic Telemetry	*Pristis pectinata*
Morel et al.	2013	Acoustic Telemetry	*Raja brachyuran* *Raja microcellata*
Couturier et al.	2013a	Stable Isotope	*Mobula alfredi*
White et al.	2013a	Acoustic Telemetry	*Glaucostegus typus* *Rhynchobatus* spp.
Cerutti-Pereyra et al.	2014	Acoustic Telemetry	*Glaucostegus typus* *Himantura uarnak* *Pastinachus atrus* *Urogymnus asperrimus*
Marcotte	2014	Acoustic Telemetry	*Myliobatis tenuicaudatus*
McCauley et al.	2014	Photo ID Sonar Stable Isotope	*Mobula alfredi*
Ajemian and Powers	2014	Archival Tag	*Rhinoptera bonasus* *Aetobatus narinari*
Germanov and Marshall	2014	Photo ID	*Mobula alfredi*
Braun et al.	2014	Archival Tag	*Mobula alfredi*
Jaine et al.	2014	Archival Tag	*Mobula alfredi*
Thorrold et al.	2014	Archival Tag	*Mobula tarapacana*
Davy et al.	2015	Acoustic Telemetry	*Himantura granulata*
Omori et al.	2015	Archival Tag	*Rhinoptera bonasus*
Braun et al.	2015	Acoustic Telemetry Archival Tag	*Mobula alfredi*
Gutteridge et al.	2015	Acoustic Telemetry Archival Tag	*Pristis pectinata*
Otaki et al.	2015	Acoustic Telemetry	*Dasyatis akajei*
Sellas et al.	2015	Genetics	*Aetobatus narinari*
Pinto et al.	2016	Archival Tag	*Dipturus intermedia*

Chapter 3

Are We Underestimating Elasmobranch Abundances on Baited Remote Underwater Video Systems (BRUVS) Using Traditional Metrics?

Plate 3. Baited remote underwater video system (BRUVS) deployment and retrieval in Borneo, Malaysia (top left = Dave McCann preparing bait; top right = a BRUVS buoy at Boheydulong; bottom left and right = BRUVS retrieval; November 2015).

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3.1 Introduction

Video from Baited Remote Underwater Video Systems (BRUVS) is increasingly being used to assess fish communities and biomass (Cappo et al. 2001; Harvey et al. 2013; White et al. 2013a; Espinoza et al. 2014), and animal behaviour (Watson et al. 2010; Hill et al. 2014). BRUVS collect a large amount of data and due to the abundance of data, several methods for analyses have been developed. The most commonly used metric is MaxN (Cappo 2010; Whitmarsh et al. 2016), which is a metric of species local abundance based on the maximum number of individuals observed in a single frame of video (Ebner et al. 2009; Louiseau et al. 2016). Use of MaxN as an estimate of abundance is common because it is relatively simple, fast, and easily comparable to other BRUVS analyses due to its wide use (Willis and Babcock 2000; Cappo 2010). MaxN is the most conservative estimate for total number of individuals from a species observed within a single BRUVS deployment (Whitmarsh et al. 2016) and is designed to eliminate double counting and overestimating abundance. The inability to easily distinguish between individuals of the same species on BRUVS videos means that it is not possible to assume that each appearance represents the arrival of a unique individual. As such, MaxN is likely to underestimate the true abundance of individuals in a single deployment (Kilfoil et al. 2017). Other methods of analysing BRUVS footage include mean count (MeanCount), time in – time out (TITO), and time of first arrival (T1st). MeanCount uses the number of individuals in frame at a given interval (5, 10, 30 s, etc.), to estimate abundance over time of species' presence (Cappo et al. 2011). However, MeanCount may miss individuals that pass quickly in front of the camera. TITO involves notation of the time of entry and exit of each animal included in the study, which is mostly used in behavioural analyses (Schobernd et al. 2014). Finally, T1st refers to the first entry of a species in the video, indicating the distance the animal was to the system and/or the attractiveness of the bait (Campbell et al. 2015). MaxN and MeanCount methods are used

to estimate abundance and diversity of species in videos, while TITO allows for behavioural analyses like boldness using the time spent openly in view of the camera (Cappo 2010) and T1st can indicate species with better olfactory abilities based on arrival times to the BRUVS (Bassett and Montgomery 2011).

While studies have compared BRUVS analysis methods to one another (Stobart et al. 2015), few have attempted to identify and count individuals to estimate true abundance (Harasti et al. 2016; Kilfoil et al. 2017). Previous studies have used unique markings to determine movement speed of individuals, but did not attempt to quantify the number of distinct individuals (Schobernd et al. 2014; Campbell et al. 2015). One recent study identified white shark individuals on Stereo-BRUVS, which revealed individuals were not occurring on multiple BRUVS deployed at the same time (Harasti et al. 2016). Identification of unique individuals via static photography has been used to help assess populations. Photo identification of individuals is commonly used in species with unique physical features and applied to a range of taxa including cetaceans (Evans and Hammond 2004; Thompson and Wheeler 2008), birds (Arroyo and Bretagnolle 1999; Williams and Thomson 2015) reptiles (Bradfield 2004; Reisser et al. 2008). Photo ID has also been used extensively in elasmobranchs. For example, in white sharks (*Carcharodon carcharias*) physical features (dorsal fin markings, injuries, size, etc.) have been used to identify individuals across multiple years (Domeier and Nasby-Lucas 2007; Ryan et al. 2015). In manta rays (*Mobula* spp.) and zebra sharks (*Stegostoma fasciatum*) colour patterns and spots unique to each individual have been used for identification of individuals (Dudgeon et al. 2008; Germanov and Marshall 2014). In BRUVS footage, multiple angles of an individual are often seen enabling detection of distinguishing features making identification of individuals possible in some species.

Surveying batoid (rays, skates, and guitarfish) populations is challenging due to their often cryptic nature and caution around larger animals, including humans (Cappo et al. 2001; Harvey et al. 2013; White et al. 2013a; Espinoza et al. 2014). Currently, fishing surveys are the most commonly used method to estimate ray population abundances and how they change through time. Fisheries sampling bias through targeting desirable species, preferentially fishing in certain areas, gear selectivity, and data limitations mean that catch data may not adequately represent ray diversity (Walker and Hislop 1998; Graham et al. 2001). However, emerging methodologies such as fishery-independent BRUVS can overcome some of these issues, and are a low impact means of sampling ray populations (White et al. 2013a). As many ray populations are currently decreasing at a rapid rate globally and are also poorly studied (Dulvy et al. 2014), there is a need for accurate abundance estimates to help inform management and conservation efforts. The aims of this study were to: a) determine if individual rays could be distinguished in BRUVS footage, and b) examine differences in MaxN compared to results from counts of identified individuals. It was expected that species with unique markings would be able to be distinguished using BRUVS footage and MaxN would significantly underestimate the true abundance.

3.2 Methods

3.2.1 Study Site

Three sites in Malaysian Borneo (Tunku Abdul Rahman Park (TARP), Tun Sakaran Marine Park (TSMP) and the islands of Mabul and Kapalai (MK)) were sampled with BRUVS. All sites consisted of patchy coral reefs with varying degrees of reef degradation within each site. The TARP (5°59’22.06’’N, 116°1’25.28’’E), established in 1974, is located 3 km off the coast of Kota Kinabalu and consists of five islands over an area of 49 km^2: Gaya, Sapi, Mamutik,

Manukan, and Sulug. The TARP is closed to fishing, however many recreational water activities occur in the park such as SCUBA diving, snorkelling, and parasailing. The TSMP (4°38'21.52''N, 118°44'0.13''E) is located 18 km northeast of Semporna and was established in 2004. The TSMP has an area of 101 km^2 and consists of seven islands and one patch reef: Boheydulong, Bodgaya, Sabangkat, Salakan, Maiga, Sibuan, Mantabuan, and Church Reef. The TSMP is restricted to subsistence fishing, however, the enforcement level is low (Sherman pers. obs.). The main activities in the TSMP include scuba diving and snorkelling. Mabul and Kapalai (4°13'49.12''N, 118°39'19.55''E) are located 25 km south of Semporna and consist of an area ~20 km^2. Both islands are open to fishing, however, they are mainly used for SCUBA diving with > 25 operators in the area. Subsistence fishing occurs daily with occasional trawlers operating within 1 km of the islands.

3.2.2 Sampling

Baited remote underwater video systems (BRUVS) were deployed during daylight hours in a variety of habitats including fore reef, reef crest, reef flat, and lagoon at depths from 1.5 m to 40 m. BRUVS used in this study consisted of aluminium frames that housed a GoPro Hero 4 Silver camera with wide angle view (approx. 170° in air), (1920 × 1080 video format, 30 frames/s) housed in NiMAR housings, and a bait arm that extended 1 m from the camera. The bait arm held a mesh bag containing approximately 1 kg of crushed pilchards (*Sardinella* spp.) or slimy mackerel (*Scomber australiasicus*). BRUVS were manually lowered to the seafloor and recovered using floating rope attached to a surface buoy marking the location. Six BRUVS were deployed at one time with each BRUV left to record video footage throughout a minimum 60 min deployment period. BRUVS were deployed with a minimum of 500 m between each BRUVS, a distance at which it was assumed that rays would not swim between adjacent cameras within the deployment period. Up to 24 BRUVS were set in

a single day through multiple tidal states with fresh bait used for each deployment. During deployments the boat maintained a distance of at least 200 m to reduce any effects of boat noise on animal behaviour.

3.2.3 Video annotation

All BRUVS footage was watched by two independent, trained annotators using Event Measure software (www.seagis.com v.4.43). Annotators marked the arrival time of every ray that entered the screen throughout the video. A senior reviewer validated species identification and compared the two reads of each video. If the two reads differed, a third independent annotator was used to determine which of the first two reads was correct. Of 286 videos, 11 required a third reader. In all 11 cases, the third reader's results matched one of the first two annotations, therefore this was deemed the final annotation. This indicated consistent and reliable results from the trained annotators.

3.2.4 Species

Two ray species were examined for this study; the oriental bluespotted maskray (*Neotrygon orientalis* Last, White & Séret 2016), and the bluespotted fantail ray (*Taeniura lymma* Forsskål, 1775). These species were selected because they were the two most frequently observed rays on Malaysian BRUVS.

3.2.5 Individual identification

To investigate how many different individuals were present, all videos with *N. orientalis* and *T. lymma* were reanalysed. Each time a ray was within the field of view, the best possible frames were extracted from the video to illustrate key identifying features (**Fig. 3.1**). Frames were then compared to differentiate between individuals within each deployment. When

individuals were not identifiable (too distant or moving too quickly) they were labelled as "unknown." No studies have been performed to determine the longevity and reliability of re-identification using markings of either species of ray in this study. However, the maximum time in which the rays could be re-identified was 90 min, therefore it was concluded that these features would not change in this time period. No attempt was made to identify individuals across deployments.

Individual *N. orientalis* were most readily identified by their unique "barcode" markings on their tails and secondarily by spot patterns on the pectoral fins (**Fig. 3.2**). In *T. lymma* tail imperfections and sex were most frequently used to distinguish individuals. Spot patterns were rarely used for *T. lymma* as the blue spots were visible only when an individual was slowly moving close to the camera which did not occur often. *Neotrygon orientalis* individuals were more easily distinguished than *T. lymma* because they had more easily distinguishable tails.

3.2.6 Analyses

Paired t-tests (R v0.99.491) were used to determine differences in number of times a ray was in frame during a deployment and the number of occurrences of distinguishable individuals for both species. Additionally, paired t-tests were used to determine if the MaxN from each video was significantly different than the number of individuals identified (MaxIND) using morphological traits for both species. Two-way ANOVA was used to determine if there was a site or species effect on the proportion of sightings of distinguishable individuals that could be identified.

3.3 Results

A total of 312 BRUVS were deployed throughout this study. Due to low visibility (< 1 m), 26 videos were removed from analysis leaving 97 from TARP, 96 from TSMP, and 67 from MK for a total of 286 successful BRUVS. From these 286 deployments, 372 occurrences of *Neotrygon orientalis* and *Taeniura lymma* were recorded. Overall, *T. lymma* were present in more videos (22.6%) than *N. orientalis* (12.3%).

From 372 occurrences of these two ray species, 282 could be identified to the individual. In *N. orientalis,* 64 occurrences were made by individuals only appearing once, 22 individuals passed through the frame twice in a video, and 17 individuals occurred 3+ times in a single video, for a total of 103 unique individuals identified. In 55 cases *T. lymma* individuals occurred once in a video, 7 individuals occurred twice, and 5 individuals occurred 3+ times in a single video for a total of 67 unique individuals identified. A significant number of rays moving through the frame were not able to be distinguished from other individuals for both species (*N. orientalis*: $t = 2.24$, $df = 32$, $p = 0.0323$; *T. lymma*: $t = 4.69$, $df = 58$, $p < 0.0001$)(**Fig. 3.3**).

A MaxN of two and three occurred 12.1% and 9.1% of the time, respectively. Throughout the three sites, *T. lymma* occurred on more deployments, but in lower numbers than *N. orientalis*. In 96.6% of videos the MaxN of *T. lymma* was one (a single individual present in the frame). Two videos had a MaxN of two. *Neotrygon orientalis* had a MaxN of one 78.8% of the time.

Use of MaxIND resulted in significantly greater numbers of both species being recorded than using MaxN (*N. orientalis*: $t = 3.59$, $df=32$, $p=0.0010$; *T. lymma*: $t=2.19$, $df=58$,

p=0.0327)(**Fig. 3.4**). Overall, MaxIND estimates were 2.4 X greater than MaxN from all videos for *N. orientalis* (**Fig. 3.5**) and 1.1× greater for *T. lymma*. Time between re-sighting of the same individual ranged from 1 s to 22.1 min in *N. orientalis* and 1 s to 49.7 min for *T. lymma*. There was also no significant difference in the proportion of identified individuals of the two species or among the three sites (*N. orientalis*: F2,85 = 0.3730, p = 0.5430; *T. lymma*: F2,85 = 0.0293, p = 0.9711)(**Table 3.1**). The largest difference in a single deployment occurred for *N. orientalis*, which had a MaxN of 3 and a MaxIND of 17.

3.4 Discussion

The results of this study quantified the potential for abundance underestimation in the most widely used metric of relative abundance in analysis of BRUVS data, indicating that MaxN can underestimate the true values of abundance by 2.4× for some species. While MaxN is commonly used for abundance estimates as it is simple and fast (Cappo 2010), it includes uncertainty when individuals swim in and out of frame. In these cases, it may be a single individual circling or multiple individuals swimming past. In contrast, counting each individual that enters as a new individual could substantially overestimate true abundance. Using MaxN removes the risk of overestimation as only the maximum number of individuals in a single frame are counted. Therefore trade-offs in analyses and outcomes need to be considered when selecting analysis methods.

BRUVS studies can be used to help detect marine reserve effects (Goetze and Fullwood 2012; Espinoza et al. 2014; Hill et al. 2014; Schobernd et al. 2014; Whitmarsh et al. 2016). We have shown that differences between MaxN and MaxIND were consistent for both species in this study between three different sites, including two within marine reserves. Therefore, conclusions drawn about marine reserve effectiveness in previous studies that

have used MaxN remain valid even though abundance estimates have likely been underestimated.

There was no significant difference in abundance underestimation between sites, but differences between species were apparent. Abundance estimates from MaxIND were higher than MaxN by 1.1× for *Taeniura lymma* and 2.4× for *Neotrygon orientalis* revealing stark differences in outputs and conclusions about population size. However, MaxIND requires the capacity to identify unique individuals via some physical feature to produce species-specific estimates. This means that the MaxIND method is not suitable for all species, and that MaxN is a more appropriate method for analysis when individuals cannot be identified. The MaxIND method would best be used as a supplement to MaxN for species where individual identification is possible.

A further consideration is that identification of individuals requires more analysis time than MaxN alone. However, new technology such as pattern recognition and identification software may be able to reduce this time discrepancy (Siddiqui et al. 2017), and indeed, is being used for a range of sharks and rays (Marshall and Pierce 2012). Increasing camera field of view angles may also improve estimates of abundance and recognition of individuals by reducing the time 'out of frame'. For example, in some cases *T. lymma* individuals would appear early in the video and return up to 50 min later. Since the GoPro™ cameras were set with only a 170° field of view in a single direction there is no way to know how far individuals travelled when out of view before returning to the BRUVS and re-entering the camera's field of view. Use of 360° cameras may increase accuracy of abundance estimates by monitoring a greater area around the BRUV and reduce loss of individuals moving in and out of frame. 360° cameras are beginning to be used for

underwater surveys to examine habitat or fish assemblages (Sanguinetti 2013; Taylor et al. 2013). It has already been confirmed MaxN can significantly underestimate abundance, particularly in high density populations (Kilfoil et al. 2017). However, use of 360° cameras also increases costs and analysis times.

As no studies have been performed to determine the longevity and reliability of unique markings used to re-identify the species of ray in this study, distinguishing individuals beyond single deployments was not possible. In other ray species, like the spotted eagle ray (*Aetobatus narinari*) and manta rays (*Mobula alfredi* or *birostris*), spot patterns have been shown to be consistent over time (Marshall et al. 2011; González-Ramos et al. 2016). A mark-recapture study or aquarium study would need to be performed to determine if the "barcode" on *N. orientalis* is stable throughout their life. Using tail imperfections of *T. lymma* would likely not be as feasible as differences were subtle and will change throughout their lives. Stingrays have a well-documented ability to shed and regrow their spines (Johansson et al. 2004; Lowe et al. 2007), however, the healing and growth of the rest of their tail is currently unknown. If persistent distinguishing features could be identified, individuals could be counted beyond single deployments and would enable additional questions to be investigated including determining whether individuals move between BRUVS deployments and are counted multiple times, or longer term and larger scale movement patterns. Another application would be in behavioural studies, as repeated entries by the same individual can be analysed. In most current methodologies BRUVS are assumed to be set sufficiently far apart for individuals not to be recounted. Identification of individuals would facilitate analyses of foraging distances and swimming speed. When deploying BRUVS over multiple days, re-identification of individuals would also facilitate population estimates similar to mark recapture studies (Dempster et al. 2010; Pelletier et al.

2012; Koenig and Stallings 2015; Lee et al. 2015).

Although MaxIND requires more analysis time than MaxN, it's improved accuracy may be advantageous in some studies such as those focusing on rare and/or endangered species, surveying high density populations, and exploring individual behaviours. Populations of rare and/or endangered species are difficult to quantify due to zero-inflated data sets (Cunningham and Lindemayer 2005). Using MaxIND to assess and monitor these species can provide more accurate abundance estimates for populations where small differences may have great significance in management and conservation (McConville et al. 2009). Finally, MaxIND, enables observation of behaviours for individuals that repeatedly enter and exit the frame. This allows for longer observation time of each individual and may even show dominance hierarchies when multiple individuals are present simultaneously (Nakano 1995). Use of 360° cameras has also shown that species occurring in high densities are often significantly undercounted using single camera BRUVS (Kilfoil et al. 2017). Using MaxIND reduces the risk of under-counting in high density areas, where a MaxN threshold may occur. Additionally, repeated sampling using MaxIND would better show population changes over time as the abundance estimates would be more accurate.

The identification of unique individuals on BRUVS deployments demonstrated that conventional BRUVS abundance metrics may underestimate the true abundance of individuals in a single deployment. By identifying individuals through unique spot patterns, tail markings, and sex, we determined that abundance of *Neotrygon orientalis* and *Taeniura lymma* were underestimated by MaxN. Although identifying individuals achieved an estimate closer to true abundance, the time for analysis was much greater. Therefore, the benefits of identifying individuals and counting MaxIND must be considered relative to the

amount of time and effort required to collect the information and the specific research questions being addressed. Identifying individuals, although time consuming, is a valuable method and provides the opportunity to address a larger suite of questions than when applying MaxN alone. MaxIND is a useful tool when dealing with rare and/or endangered species as it will provide more accurate abundances of these species. MaxIND will also be useful for species that can be found in groups as the entire group may not be observed in the frame at a given time but counting distinct individuals will accurately reflect the abundance.

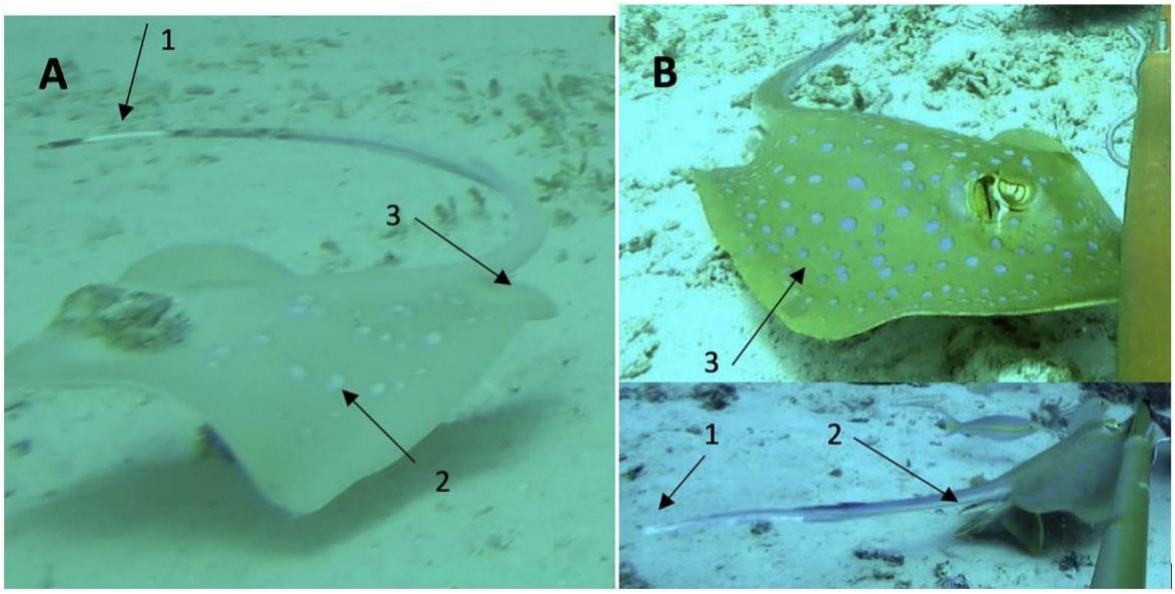


Figure 3.1. Features used to distinguish individuals of the (A) oriental bluespotted maskray: (1) "Barcode" – number of iterations of black and white, size of segments, presence/absence, (2) Spot patterns – clusters of spots, left and/or right pectoral fins, (3) Sex – male/female and (B) bluespotted fantail ray (1) Tail scratches/ bites – small imperfections in tail flap and white tip of tail, (2) Sex – male/female, (3) Spot patterns – clusters of spots, left and/or right pectoral fins, rostrum. Where possible, multiple features were used in conjunction for distinguishing individuals.

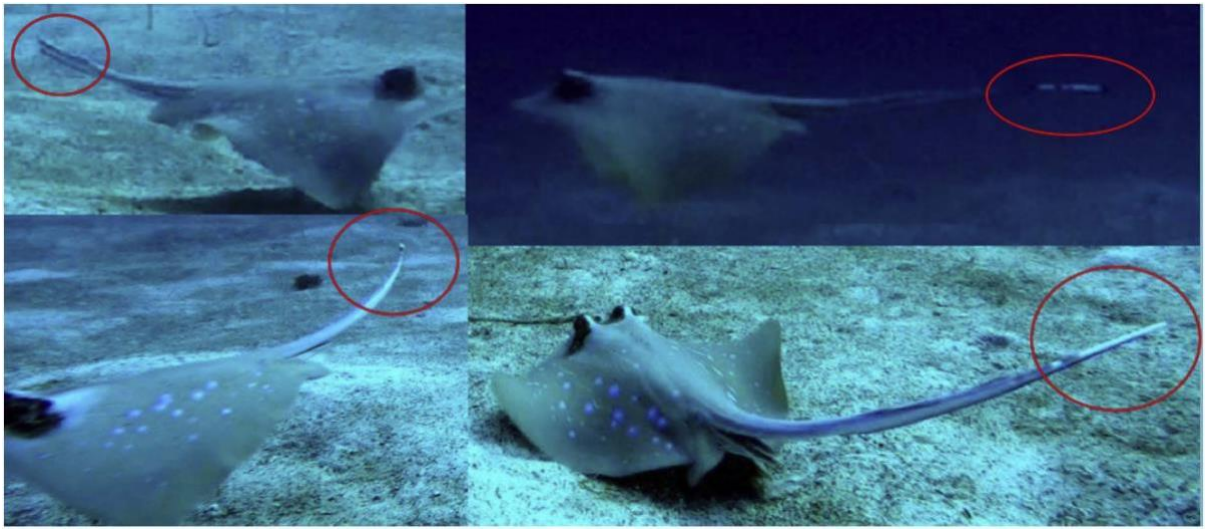


Figure 3.2. Four oriental bluespotted maskray individuals from the same video. This video had a MaxN of one, 11 rays were observed in front of the camera and four individuals were distinguished through differences in their tails.

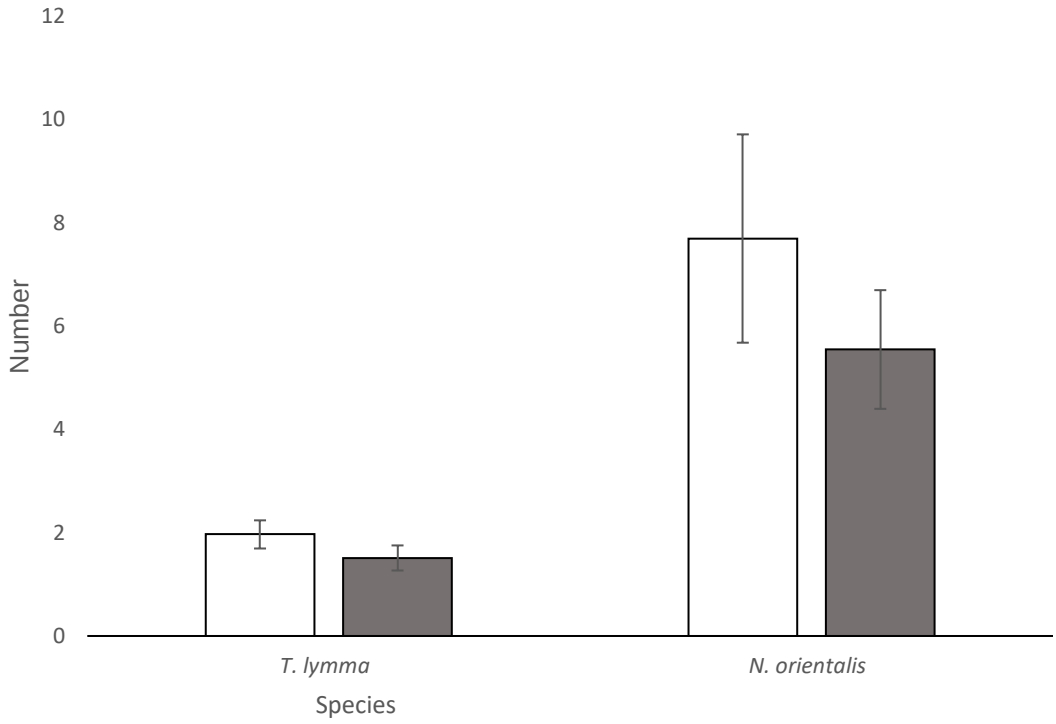


Figure 3.3. Mean numbers of identified passes by an individual in front of the camera was significantly lower than the overall number of rays that passed through the field of view in each video for both species (* $p < 0.05$; ** $p < 0.0001$). Error bars represent one standard deviation, shaded bars represent number of identified passes and white bars represent total number of total times an individual of the species was in the field of view.

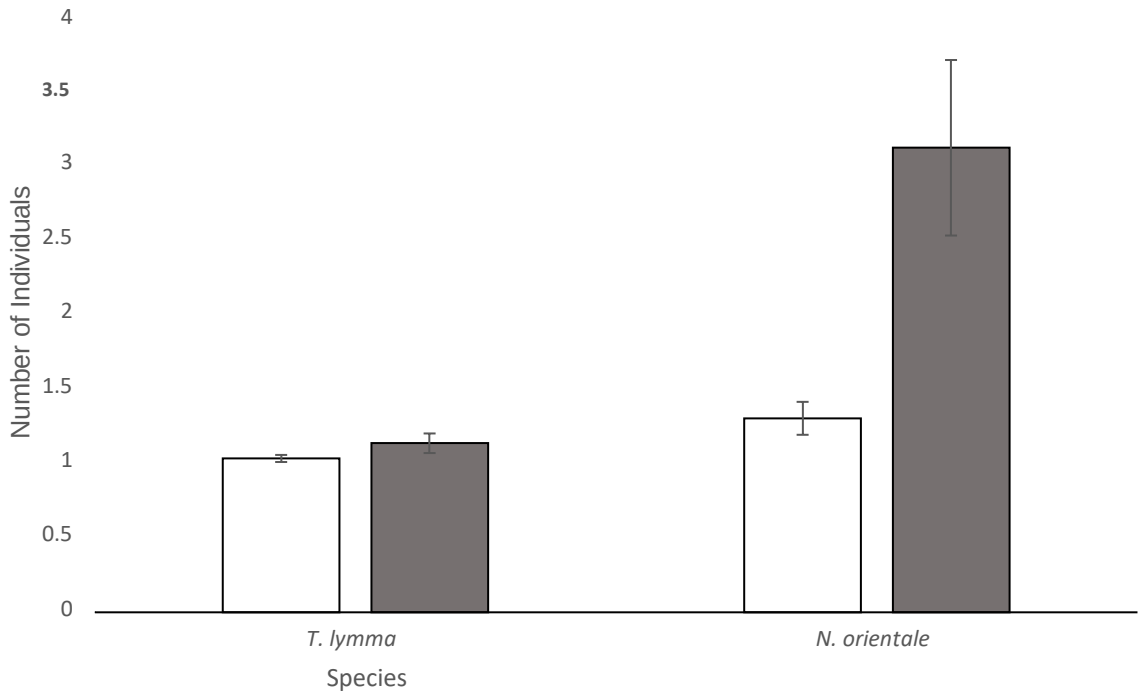


Figure 3.4. Mean numbers of identified *T. lymma* and *N. orientalis* were significantly lower than the mean number of passes made by the species (* $p < 0.05$; ** $p < 0.005$). Error bars represent one standard deviation, shaded bars represent number of identified individuals (MaxIND) and white bars represent MaxN.

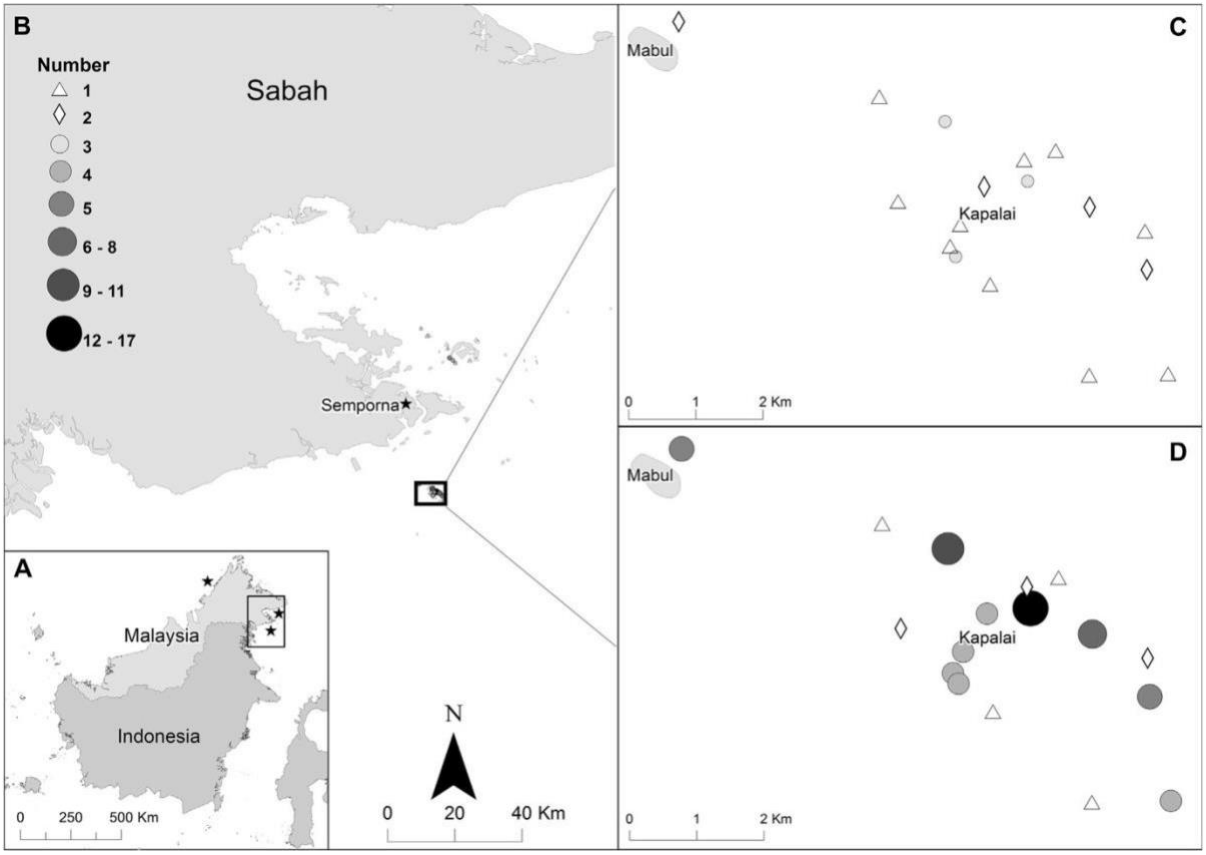


Figure 3.5. A) Borneo. Stars indicate three sampling sites in Malaysian Borneo. B) BRUVS drops off Semporna. C) MaxN of drops with oriental bluespotted maskrays present. Only videos with at least one maskray present were included. D) Number of identified individuals on BRUVS with oriental bluespotted maskrays present.

Table 3.1. *Neotrygon orientalis* and *Taeniura lymma* observations and identification at each of the three sites in this study.

Species	***Neotrygon orientalis***				***Taeniura lymma***			
Site	**TSMP**	**TARP**	**MK**	**Total**	**TSMP**	**TARP**	**MK**	**Total**
Videos present	13	2	17	32	32	19	8	59
Videos with a single pass	2	2	4	8	17	14	7	38
Total observations	58	2	193	253	76	30	10	116
Identifiable individuals	51	2	129	182	59	22	8	89

Chapter 4

Repeatability of BRUVS results within and between seasons

Plate 4. Sampling in Bau Bau Sulawesi (top left = Gerhana and Hiu Putih at Pulau Ular; top right = Squeak and Earl disassembling BRUVS equipment; bottom left = BRUVing with local university students February 2019; bottom right = Operation Wallacea staff August 2018).

4.1 Introduction

Sampling methodology that yields consistent and precise results is a fundamental aspect of ecological research (Smith and Gelfand 1992; Elphick 2008). When completing research in a lab, many environmental factors can be controlled for consistency to ensure results are a direct effect of what is being tested (Parsons and Carlson 1998). Additionally, sampling can be completed with a planned number of individuals to determine the consistency of results within a population (Walter et al. 1998; Wolak et al. 2012). In the field, researchers cannot control water conditions or chemistry, daylight hours, and other biota that may influence study species (Karl and Lukas 1996). Therefore, it is often difficult to have a completely controlled field study in a natural setting. Presenting novel equipment in an environment can also introduce a sampling bias by increasing the likelihood of encountering higher risk-takers (Stuber et al. 2013). In ecological studies, reproducible methods are one important way researchers can achieve consistent results (Cassey and Blackburn 2006; Ellison 2010).

Baited remote underwater video systems (BRUVS) are increasingly being used for sampling predator abundances on coral reefs (Whitmarsh et al. 2016; Kilfoil et al. 2017; Goetze et al. 2018). BRUVS have been shown to have higher statistical power and consistency than unbaited videos (Bernard and Götz 2012). However, immediate resampling of an area has not yet been performed to determine repeatability of BRUVS surveys for elasmobranchs or other taxa. On a temporal scale, time of day has been shown to significantly affect the species observed on BRUVS (Birt et al. 2012; Taylor et al. 2013). Only a single study has examined abundance of any species during different seasons and found season did not significantly affect presence of wedgefish (*Rhynchobatus* spp.) at BRUVS on the Great Barrier Reef (White et al. 2013a). Many BRUVS studies compare locations that are sampled at a single time point (Tickler et al. 2017; Goetze et al. 2018). By only having a single

sampling period, community composition and abundance estimates may be influenced by sampling consistency and seasonal patterns. This may present problems with interpretation of data when multiple sites that may have seasonally influenced residents are sampled during different seasons and results compared.

BRUVS sampling at different times throughout the year may show different species as some may be migratory. Seasonal movements have been documented in many marine animals with continental scale seasonal migrations occurring in many species (Eckert and Stewart 2001; Pomilla and Rosenbaum 2005; Heupel et al. 2015). Smaller scale migrations have been observed in several elasmobranch species including pelagic rays such as manta rays (*Mobula* spp.) and eagle rays (*Aetobatus* spp.)(Anderson et al. 2011a; Sellas et al. 2015; Barbosa-Filho et al. 2016). There is little information on the movement patterns of tropical benthic rays. In benthic rays, few studies have examined migratory behaviour and only in thornback rays (*Raja clavata*) has direct evidence of seasonal migration been noted (Hunter et al. 2005; Hunter et al. 2006). In tropical coral reef elasmobranchs, seasonal shark migrations have been noted in some bull sharks (*Carcharhinus leucas*) and tiger sharks (*Galeocerdo cuvier*)(Fitzpatrick et al. 2012; Werry et al. 2014; Espinoza et al. 2015). Other species, like blacktip reef sharks (*Carcharhinus melanopterus*) can exhibit high site fidelity, with some individuals also capable of making longer range movements and use both coastal and offshore reef habitats throughout their lives (Barnett et al. 2012; Chin et al. 2013).

Environmental factors are potential sources of variation in the abundance of species detected by BRUVS sampling. There are many environmental factors that can influence elasmobranch movement patterns and hence presence on BRUVS due to preferences for certain conditions (Schlaff et al. 2014). Environmental factors can have varying

levels of influence, with some being more important than others. These factors include: temperature (Sims et al. 2006; Vaudo and Heithaus 2009), salinity (Knip et al. 2011), phosphate levels (Barausse et al. 2014), dissolved oxygen (Parsons and Carlson 1998; Heithaus et al. 2009), and tide (Ackerman et al. 2000; Davy et al. 2015), among others. Many of these environmental preferences are species-specific, meaning data is required for each species to determine likelihood of encountering a species in different conditions. Even in tropical coral reef ecosystems where climactic conditions remain relatively stable throughout the year there can be significant changes to the water characteristics seasonally (Condie and Dunn 2006). Each factor can change on a wide range of time scales including daily, seasonally, and/or annually. Other influencing factors on elasmobranch presence at BRUVS may include bait and associated factors. For example, bait plume size, determined by currents and initial bait weight, can dramatically affect species and abundances observed on BRUVS (Heagney et al. 2007). Additionally, the type of bait used also effects species presence (Wraith et al. 2013). Therefore, it is important to note changes in environmental conditions and keep factors within the researcher's control, like bait type and amount, consistent to ensure repeatability.

As coral reef monitoring using BRUVS grows in its capacity to provide data relevant to sustainable management, marine protected area success, and overall reef health, understanding repeatability of sampling results is vital. BRUVS are increasingly being used for sampling coral reef species diversity and abundance for a wide range of species. Therefore, the consistency of BRUVS sampling is vital for conclusions from these studies.

The aims of this paper are to: 1) determine repeatability of results from BRUVS sampling for

elasmobranchs within and between seasons and years, and 2) determine seasonal differences in abundance, habitat use or assemblage of elasmobranchs during different seasons.

4.2 Methods

4.2.1 Study Site

This research was carried out in Bau Bau, in South Sulawesi on the island of Buton, Indonesia and has a fast-growing human population of over 150,000 (Rokhim et al. 2017). There are two distinct seasons through the year: wet and dry. The dry season begins in June lasting through November during which winds come from the southeast. The wet season begins in December and has prevailing winds from the west (Tjasyono H.K. et al. 2008). Despite having a wet and dry season, the area has heavy rainfall throughout the year with approximately 50 mm in the driest months and over 250 mm in the wettest months. Average temperature is fairly consistent at approximately 25°C throughout the year. Average water temperature ranges from 24-32°C with colder temperatures recorded in August through October (Merkel 2019). The sampling area near Bau Bau was split into two sites; one along the coast from the city centre to the southern tip of Buton, and one consisting of three islands (Kadatua, Siompu, and Pulau Ular) each approximately 5 km from the main island of Buton. Kadatua and Siompu each have a few small villages whose residents partake in subsistence fishing in adjacent waters using small vessels. Pulau Ular is uninhabited, however, many subsistence fishermen from the other islands and Bau Bau city fish around the island (pers. obs). Similar to the rest of Indonesia, the primary animal protein consumed is fish, which is incorporated into at least 2 meals per day. This demand for fish protein has led to an extremely high level of both commercial and subsistence fishing that is underreported by up to 75% (Tull 2014). In particular, shark catch has been

underreported yet they are widely targeted due to the high value of their fins (Varkey et al. 2010). Stingrays are also frequently captured and retained and sold, regardless of size or worth (Asut et al. 2019).

4.2.2 Sampling

A total of 956 successful BRUVS were deployed as per Sherman *et al*. (2018) at depths ranging from 1.5 m to 47.3 m, with an average depth of 19.7 ± 0.3 m. BRUVS were set for a minimum of one hour with an average deployment time of 75.5 ± 0.4 mins. Sampling was repeated six times: late March 2017 and 2018 (wet season), July 2017 and 2018 (early dry season) and August 2017 and 2018 (late dry season). The two dry season sampling periods (early and late) enabled evaluation of repeatability of results when abundance and species composition should be stable, making this the only way to determine repeatability. Sampling over two years allowed for analysis of repeatability between years. Finally, sampling in different seasons enabled evaluation of seasonal changes in elasmobranch abundances.

During both deployment and haul of BRUVS units, environmental factors recorded included: date, time, location (latitude/longitude), depth (m), cloud cover (%), tidal state (ebb, slack, flow), wind speed (Beaufort scale) and wind direction. Deployment times were split into three categories: morning (sets deployed before 10:29), midday (sets deployed from 10:30-13:29) and afternoon (sets deployed after 13:30).

4.2.3 Video Analysis

BRUVS footage was analysed for MaxN of all elasmobranch species using FinPrint Annotator (v.1.1.44.0). MaxN is the maximum number of individuals of a species observed in a single

video frame. This was then converted to sightings per unit effort (SPUE) by diving the MaxN by the hours of video (MaxN/hr). Video footage was watched by two independent annotators to ensure accuracy and species identification was validated by a senior reviewer. Visibility was assessed from video footage and categorised in two meter bins (0-2 m, 2-4 m, etc.) and then assigned the median value from the bin (i.e. 6-8 m bin would be assigned a value of 7).

Habitat and relief were determined by splitting the screen in a 5x4 square grid (20 squares total) using BenthoBox (www.benthobox.com). Each square within the grid that contained any benthos was assigned a relief score from 0 (flat) to 5 (complex) and the average score of all square containing relief was calculated. Reliefs with scores <1 indicate deployments in sandy habitats, whereas relief scores >2 indicate a deployment within the coral reef. Habitat was similarly assessed using the 20 squares. For each square, the majority habitat category was selected and percent cover was calculated based on the total number of squares containing benthos. Possible benthos categories were hard coral, soft coral, bleached coral, unconsolidated (sand/rubble), consolidated (rock), seagrass, turf algae, macroalgae, sponge, true anemones, ascidians, crinoids, halimeda, hydrocoral, hydroids, and invertebrate complex.

4.2.4 Species

At least 11 species of rays were observed, with up to 23 different species seen throughout the study. Identification to species level was not possible for maskrays (genus: *Neotrygon*), eagle rays (genera: *Aetobatus and Aetomylaeus*), and devil/manta rays (genus: *Mobula*)(**Table 4.1**) making the exact number of species impossible to accurately estimate. Two species of shark were observed: blacktip reef shark (*Carcharhinus melanopterus*) and whitetip reef shark (*Triaenodon obesus*). A total of 1139 elasmobranchs comprising 784 rays and 355 sharks were observed over 1202.45 hours of footage on 956 BRUVS (**Table**

4.2). Of the two shark species, blacktip reef sharks were far more abundant than whitetip reef sharks, comprising 89.0% of all sharks observed. Maskrays comprised almost half (47.1%), and fantail rays comprised a quarter (25.6%) of rays in this study. Eagle rays comprised 13.9% of rays observed. These three groups combined accounted for a large majority of rays observed (86.6%). Less than 10 individuals were observed from five different species and one genus of ray (**Table 4.2**).

4.2.5 Statistical Analysis

All statistics were performed using R (version 3.5.1) and abundances were standardized to MaxN per hour for each species / species group. Due to the low sample size of larger rays that have similar ecological niches, all benthic stingrays with maximum disc widths over 1 m were combined for analyses and called "large stingrays". A total of 95 rays in this category were observed from six species (*Himantura uarnak, Pateobatus fai, Pastinachus ater, Taeniurops meyeni, Urogymnus asperrimus* and *U. granulatus*). All shark species were also combined as a single group for analyses. This group was dominated by blacktip reef sharks (*Carcharhinus melanopterus*) and, therefore, they are likely the drivers of any patterns observed. The exact species identification of maskrays (Genus: *Neotrygon*) was not possible, therefore, all maskrays were combined for analysis. Similarly, eagle rays were often observed in the distance and it was not possible to determine species, thus all eagle rays were combined for analysis (Genera: *Aetobatus and Aetomylaeus*).

A MANOVA was used to determine any differences within and between seasons and years in sightings of each elasmobranch category (all sharks, all rays, maskrays, fantail rays, eagle rays, and large stingrays). Post-hoc ANOVA tests were performed for each species followed

by a Tukey HSD post-hoc test for each significant ANOVA to determine where differences in abundances occurred.

Generalised linear mixed models (GLMMs) were used (R package – glmmTMB (Brooks et al. 2017)) to determine environmental factors driving species abundances. All six groups of elasmobranchs were analysed. Thirty-five ecologically relevant models plus a null model were run with MaxN of each elasmobranch group acting as the dependent variable. Models included the environmental variables recorded in the field, as well as shark presence (for models pertaining to ray presence only). The most parsimonious model within two Aikaike Information Criterion (AIC) units of the best performing model was selected (Akaike 1998; Burnham and Anderson 2004). Variance inflation factors (VIF) were performed on all models to ensure there was no collinearity between variables (Akinwande et al. 2015). Three distributions (negative binomial, zero-inflated negative binomial, and poisson) were tested for each species / species group and the best performing distribution, based on AIC and a Vuong test, was used for all models in that species / species group. Generalised boosted regression models (GBM) were performed in order to determine level of contribution of each factor included in selected models (R package – gbm (Greenwell et al. 2018)). GBMs were run with the inclusion of all BRUVS deployments, a tree complexity of 5, computer learning rate of 0.001, and a bag fraction of 0.5.

PRIMER 7 was used to determine differences in species composition between seasons, years, and sites. The abundance of each species (except maskrays, eagle rays, and manta/ devil rays, which were identified to genus) was calculated for 12 groups (every combination of season – wet, early dry, late dry; site – islands and coast; and year – 2017 and 2018). Abundances were square root transformed to reduce the leverage of the more commonly

observed species. Resemblance was analysed between samples using Bray-Curtis similarity. A SIMPROF (similarity profile test) was performed to determine if significant clusters were formed in species composition between the 12 groups. The SIMPROF was performed using Bray-Curtis similarity matrix and clusters were examined at $p<0.05$ with a maximum of 4,999 permutations. A non-metric multi-dimensional scaling (nMDS) plot was created based on the resemblance values of the 12 groups with a minimum stress of 0.01 and 50 restarts.

4.3 Results

4.3.1 Temporal Variations in Abundance

There were significant temporal differences in the abundances of the six species/ species groups of elasmobranchs analysed (**Table 4.3**). Season significantly affected abundances of elasmobranchs, however, year and an interaction between year and season did not show significant differences (**Table 4.3**). Post-hoc ANOVAS indicated that different abundances between years were only present in a single group, the eagle rays, which significantly decreased in abundance from 2017 to 2018 (**Table 4.4**). Seasonal differences in abundance were found for four of the species/ species groups using a post-hoc ANOVA. All sharks, all rays, maskrays, and bluespotted fantail rays had significant seasonal changes in abundance between seasons (**Table 4.4, Fig. 4.1**). Tukey post-hoc tests indicated the differences in abundance for each group were between the wet and early dry, and wet and late dry seasons (all $p<0.05$). There were no significant differences in abundance for any species between the early dry and late dry seasons (all $p>0.05$)(**Fig. 4.1**). As both early and late dry seasons provided the same abundances for each species/ species group, they were combined to a single 'dry season' for analysis of environmental factors affecting abundance.

4.3.2 Environmental Influences on Abundance

Generalised linear mixed effects models (GLMMs) showed season, relief, reef, and depth to be significant factors contributing to ray presence and abundance. Varying combinations of those factors were important to different species/ species groups (**Table 4.5**). Visibility was also a contributing factor in the top model for eagle rays. Eagle rays were often observed incidentally in the distance, therefore, this inclusion in the top model was expected. For large stingrays, the top performing model was the null model (**Table 4.5**), indicating there was no evidence that environmental factors had anything other than random effects on this groups of species when analysed together.

All sharks, all rays, maskrays, and fantail rays had higher MaxN values in the wet season than the dry season (**Figs 4.2-4.4**). Site was also an influencing factor on abundance for four species/ species groups (all sharks, all rays, fantail rays, and eagle rays). These four groups were all significantly higher in abundance at the islands site than the coast site (**Figs 4.2-4.4**).

Generalised boosted regression models (GBMs) showed relative influence of relief was the greatest contributing variable for all sharks and maskray abundances (70% and 56%, respectively), and was also high for all rays (39%)(**Fig. 4.5**). Depth was the greatest or second greatest contributing variable (over 35%) for all rays, fantail rays, and maskray abundances. Both reef and season were contributing variables in four of the six species/ species groups. For eagle rays, visibility was the highest contributing variable at 64% (**Fig. 4.5**).

Sharks were observed in higher abundances on the western side of each island and Buton in both the dry and wet seasons (**Fig. 4.2**). This was more apparent in the wet season when the winds come from the west, likely causing upwellings and, therefore, higher fish biomass (Imin Kaimuddin, pers. obs). The two species of rays that were most commonly observed had opposing habitat preferences. Higher sightings of fantail rays were observed in areas with healthy coral reef habitat and higher abundances of maskrays were observed in sandy habitats, with little overlap of the two species (**Fig. 4.4**). There are higher concentrations of coral reefs at the islands site associated with higher abundances of fantail rays at the islands than the coast. Similarly, the coast consists of a few reef patches and mostly sandy habitat leading to higher abundances of the maskrays (**Fig. 4.2**).

4.3.3 Elasmobranch Assemblage

A SIMPROF on 12 groups (all combinations of season, site, and year) indicated a significant difference in elasmobranch assemblage between the coast site and islands site (N permutations = 4,999, $p = 0.007$). No other significant clusters formed with either year or season (N permutations = 4,999, all $p > 0.321$; **Fig. 4.6**). An nMDS plot also showed a divide between elasmobranch assemblage at the islands and at the coast (**Fig. 4.7**). The groups from the wet season, although not tightly clustered, were also separated from the two dry season sampling periods.

4.4 Discussion

The results of this study show that BRUVS are a fitting survey method to capture spatial and temporal variation in assemblages. Due to their effectiveness, repeatability of sampling can be determined. In this study, we showed that BRUVS deployed in the same location, even when performed immediately after initial sampling, can provide consistent results for both

elasmobranch abundance and assemblage. Distinct seasonal difference in abundances of sharks and rays on coral reefs in Bau Bau, Indonesia were observed and this difference is repeated in subsequent years. BRUVS are proven to be a reliable sampling method for abundance and assemblage comparisons in this study. However, seasonal differences may need to be accounted for when comparing locations throughout the year. Elasmobranch assemblage did not change significantly between seasons indicating a consistent elasmobranch community. This result was expected as there are no known migratory elasmobranch species in the area. This also suggests that any seasonal differences observed were the result of changing abundances of each species within the elasmobranch community. However, the reason for these differences in abundance is unknown.

Seasonal differences in abundance seemingly contradict existing data that show blacktip reef sharks, bluespotted maskrays, and bluespotted fantail rays are highly reef associated and non-migratory species (Papastamatiou et al. 2009; Pierce and Bennett 2009; Last et al. 2016). Blacktip reef sharks comprised 89% of sharks observed in this study and have not been observed to be seasonally migrant in other regions of the world (Barnett et al. 2012). Females have been documented to make movements of up to 50 km from their home range for parturition (Mourier and Planes 2012). This may explain the reduced abundances if females are moving for parturition. However, the change in abundance observed was high and likely not fully explained by female movement. Additionally, juvenile blacktip reef sharks have been observed in the area, suggesting the area contains viable habitat for juveniles. The waters surrounding Bau Bau have high concentrations of mesophotic corals (Erika Greiss, pers comms), meaning higher abundances of fish can be supported in deeper waters providing food sources for sharks. However, water temperatures are cooler in the dry season, thus it seems unlikely sharks would spend time in deeper, cooler water as

previous studies have provided evidence of behavioural thermoregulation in this species (Speed et al. 2012). Further research is needed to determine the movement patterns of reef sharks surrounding Bau Bau and additional environmental variables should be tested across seasons to gain a better understanding of why their abundances appear different on BRUVS between seasons.

Bluespotted maskrays comprised 47% of all rays observed and although no data on their movement patterns exist, one study captured individuals after 3 years of liberty within 40 km of where they were tagged, suggesting relatively small home ranges (Pierce and Bennett 2009). There is no distinct breeding season in maskrays and in a captive population, mating occurred soon after parturition (Janse and Schrama 2010). Therefore, movement for mating seems unlikely and would not explain the patterns observed here. These rays occur in high abundances in Southeast Asia in sandy habitats adjacent to reefs where they can feed on benthic, sand-dwelling invertebrates (Sherman et al. 2018). The second most abundant species of ray, the bluespotted fantail ray, comprised 26% of rays observed. These rays are extremely dependent on coral reefs as they use corals for protection while resting, suggesting that movement away from their reef is unlikely between seasons (Last et al. 2016).

Abiotic factors may play a large role in the ability to observe elasmobranchs on BRUVS between the different seasons. In the wet season, the prevailing wind is from the west, when higher abundances of sharks were observed. Wind speed and duration can greatly affect the nutrient loading in a region (Feng et al. 2012). Despite the wind changes, visibility was not significantly different between seasons, therefore, this was not a contributing factor in the different abundances observed. While this may provide some explanation for

why sharks were observed on the western side of the islands, individuals do not appear to shift to the east side of the smaller islands in the dry season when winds change. Reef sharks are able to travel further than rays, so it is possible that a portion of the population seasonally migrates to the east side of Buton, which was not sampled in this study. This seems unlikely, however, as that distance can be up to 80 km, much further than documented movements (Papastamatiou et al. 2010; Chin et al. 2013).

Although the area has a relatively stable temperature throughout the year, nutrient loads may still be affected by winds and other environmental factors during different seasons (D'Croz and O'Dea 2007). South Sulawesi has a noted peak in chlorophyll *a* around July, during the dry season sampling period (Condie and Dunn 2006). Dissolved oxygen levels can dramatically shift diurnally in these eutrophic periods with high oxygen levels during daylight hours when photosynthesis is occurring and low oxygen levels at night (Reyes and Merino 1991). Changes in oxygen levels may be affecting shark and ray movement, and therefore, their detectability on BRUVS. With lower oxygen levels at night in the dry season, elasmobranch activity may be reduced during the day. For example, in the bonnethead shark (*Sphyrna tiburo*) lower dissolved oxygen levels led to increased swimming and higher activity rates (Parsons and Carlson 1998). There may be fewer individuals observed in the dry season as they move more at night, to account for the lower oxygen levels. Oxygen consumption in elasmobranchs has been shown to increase with increasing temperature (Hopkins and Cech Jr. 1994), therefore, sharks and rays may have higher activity rates in the warmer months (wet season) due to increased oxygen consumption. Additionally, as ectotherms, elasmobranchs may be more active due to the increase in temperature (Papastamatiou et al. 2015). With higher activity levels (movement), there would be a higher likelihood of encountering a bait plume and following it to the BRUVS. As no studies

have been performed on the metabolic rate of the focal species in this study, it is unknown how they are affected by changes in oxygen levels.

Time of day was not a significant factor in the presence of any elasmobranch species, however, sampling in this study only occurred during daylight hours. Some elasmobranch species, like whitetip reef sharks are nocturnal feeders so may not be attracted to bait set during daylight hours (Fitzpatrick et al. 2011). Few whitetip reef sharks were observed in this study, potentially because they were not actively hunting during BRUVS deployment times (Whitney et al. 2007). Stingray diel patterns are not well studied and there are apparent species-specific differences in total activity diurnally, with some more active at night and others consistently activity throughout the day (Cartamil et al. 2003; Brinton and Curran 2017). No movement information on the ray species observed in this study was available.

There were significantly higher abundances of sharks and rays at the islands site, which was likely the result of higher fishing pressure at the coast site. Sharks have been shown to be more abundant in areas with lower human populations (Cinner et al. 2018). The coast has a much higher population than any of the three islands, two of which are inhabited with a few small villages. The primary fishing vessels used in the Bau Bau region are small dugout canoes, sometimes with a small motor (pers. obs). These canoes are not powerful enough to travel from the coast to the islands for fishing. Therefore, only larger boats and island locals are able to fish at the islands site. Additionally, due to the large population in Bau Bau, the coast is subject to high levels of contamination from sewage, rubbish, noise, and other pollutants that may affect elasmobranch abundances (Simmonds et al. 2014; Baum et al. 2015). These pollutants may also affect the habitat quality, therefore, the island sit likely has

preferable habitat. Although not remote, this shows that ease of access to fishing grounds and other anthropogenic impacts can greatly impact species composition and abundance. With technological advances in fishing rapidly increasing, more areas will be subject to higher fishing pressure (Walsh et al. 2002; MacLennan 2017), this will continue to affect elasmobranch assemblage.

In conclusion, the results from this study demonstrate that while BRUVS are a consistent, reliable and repeatable method for surveying elasmobranchs, care must be taken in timing of sampling various regions to ensure accuracy when comparing multiple locations. Although the site sampled was tropical with minimal seasonal changes in temperature and weather conditions, there were significantly different abundances of both sharks and rays across seasons. This suggest that cross-site comparisons should be performed in the same season to achieve accurate comparisons. Further investigation analysing invertebrate and fish biomass, dissolved oxygen, and other environmental variables should be done to determine if these may be influencing elasmobranch presence or catchability throughout the year.

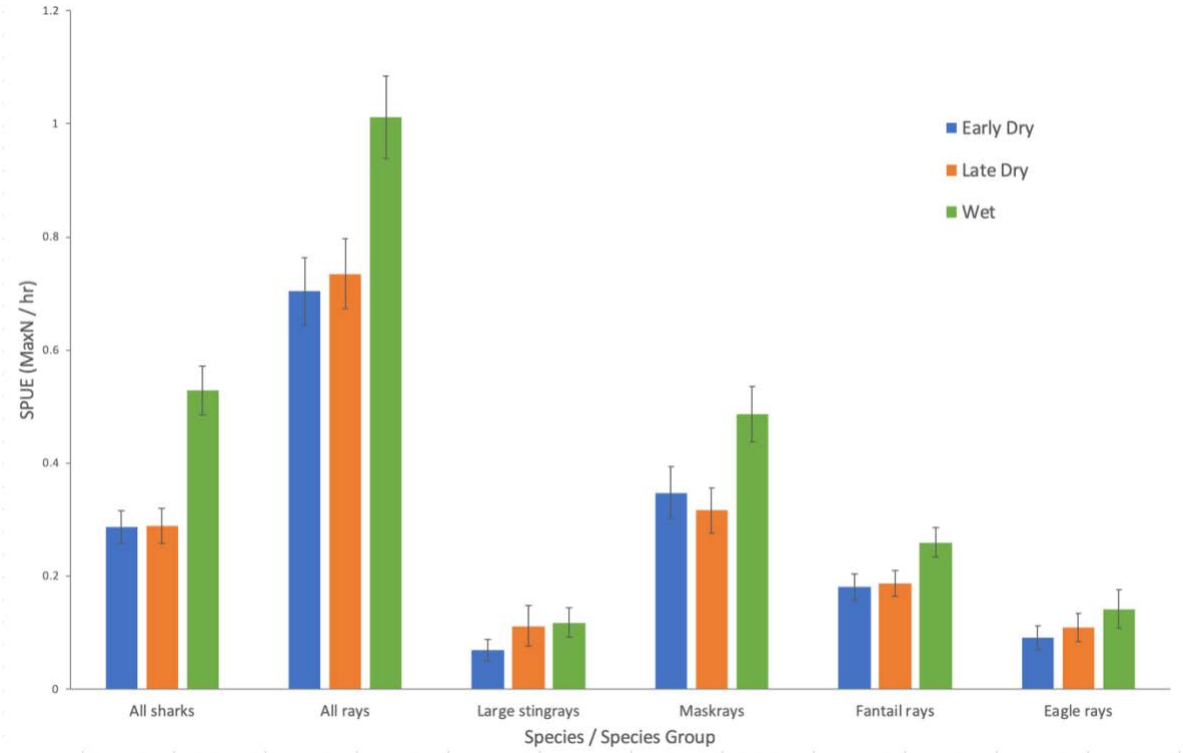


Figure 4.1. Sightings per unit effort (MaxN / hour) of the six different species/ species groups analysed. All sharks, all rays, maskrays and bluespotted fantail rays had significantly higher abundances in the wet season than both the early and late dry season as per a MANOVA, follow up ANOVA and Tukey post-hoc analyses.

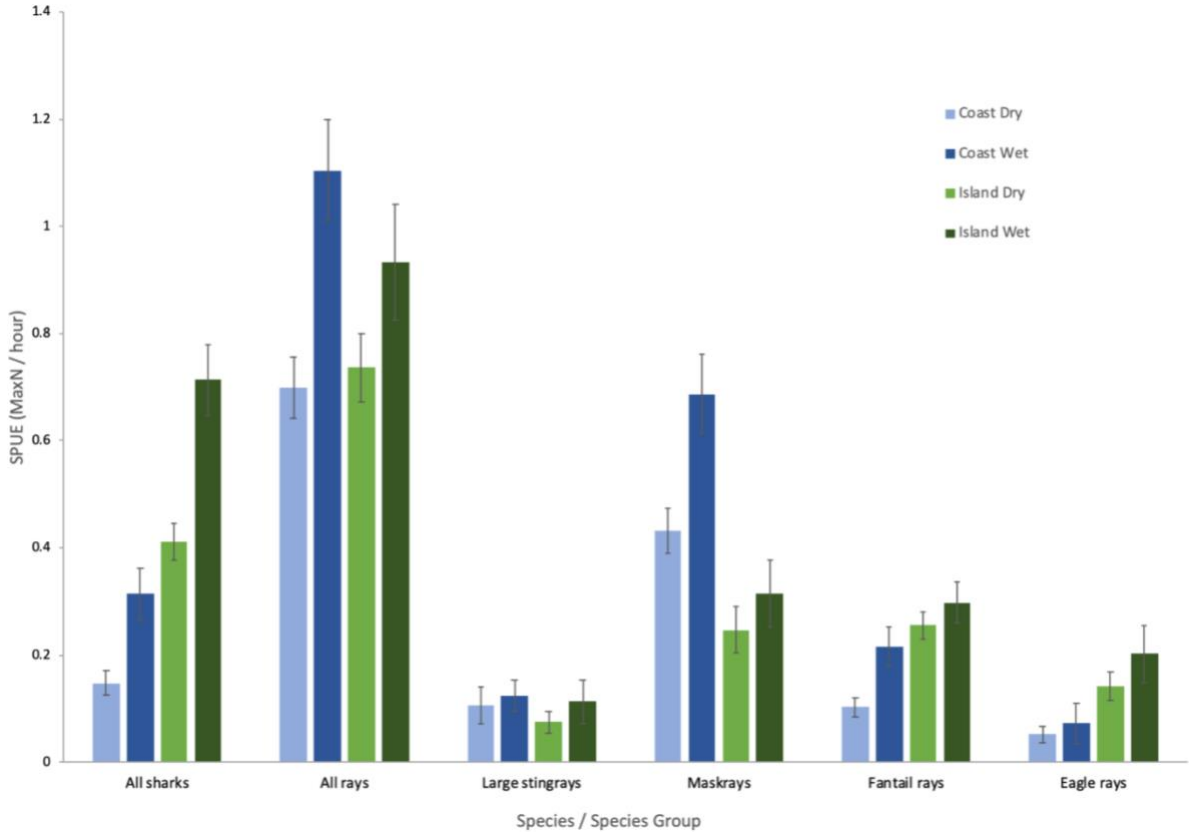


Figure 4.2. Sightings per unit effort (MaxN / hour) of the six different species/ species groups analysed at the two reefs in both seasons (early and late dry seasons are combined). Season was a significant influencing factor in abundance for all sharks, all rays, maskrays, and fantail rays will all four species/ species groups having higher abundances in the wet season.

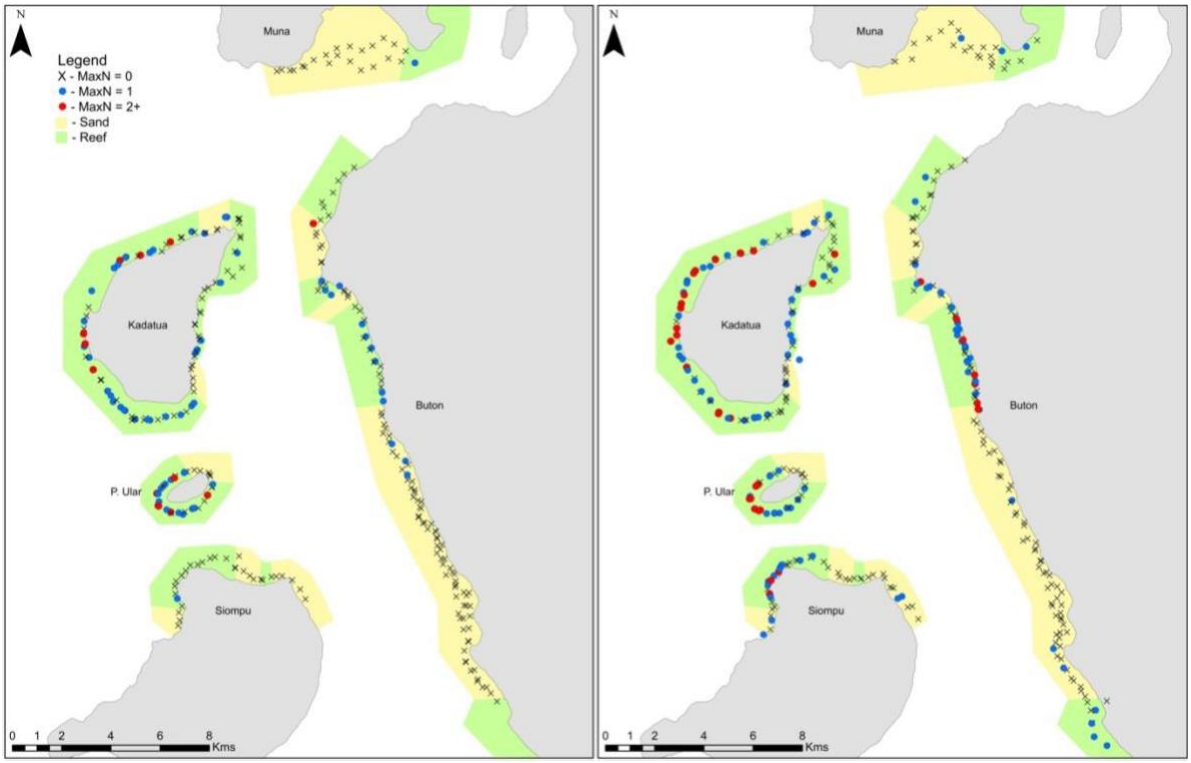


Figure 4.3. Presence of sharks in Bau Bau, Sulawesi, Indonesia in the late dry (left), and wet (right) seasons. Sightings were significantly higher in the wet season than both dry seasons, which were not statistically different from one another. Higher concentrations of sharks were observed on the western side of each island, particularly in the wet season. Black Xs indicate BRUVS deployments with no sharks, blue circles indicate deployments with a single shark, while red dots indicate deployments with multiple sharks present.

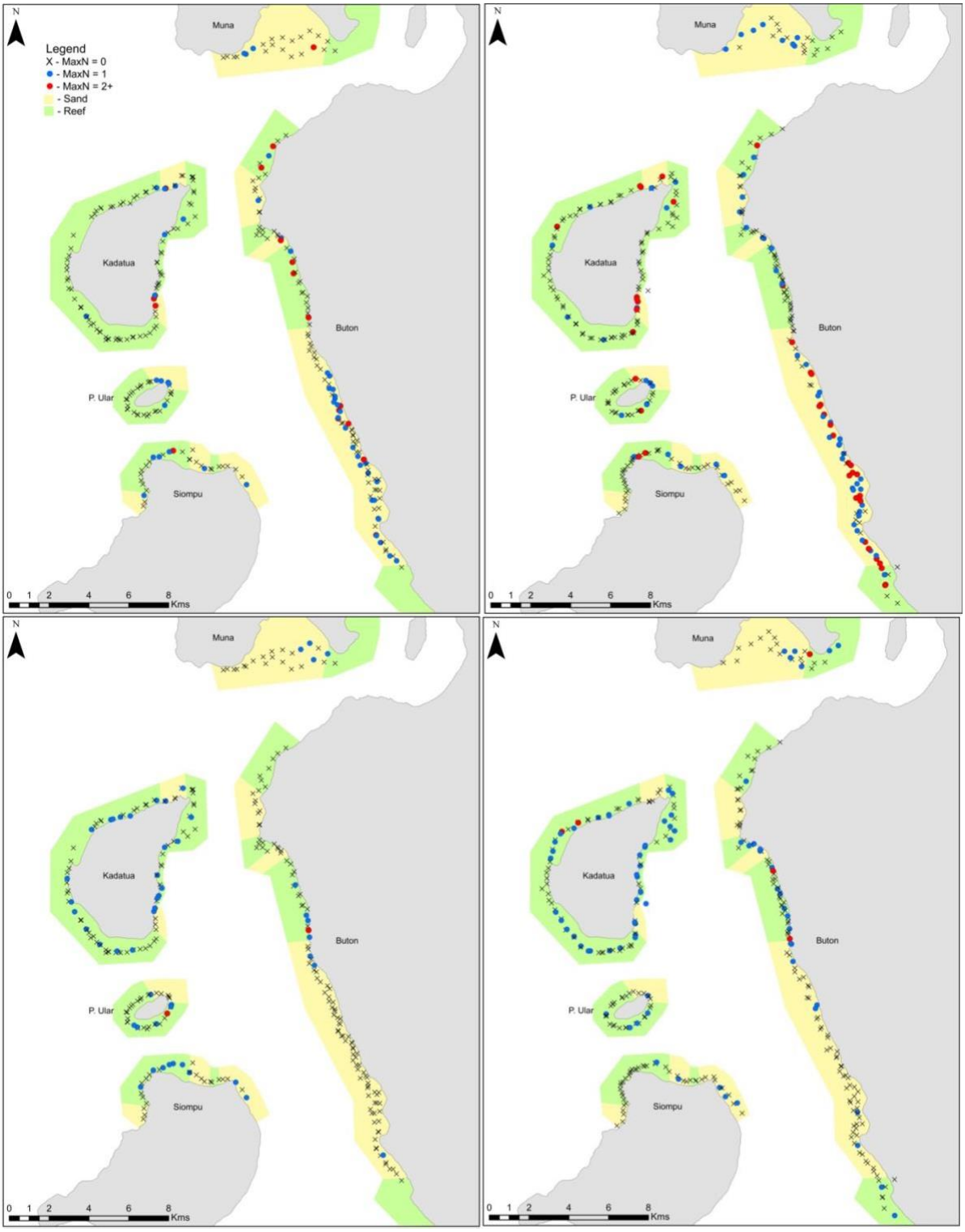


Figure 4.4. Sightings per unit effort (SPUE) of bluespotted maskrays (*Neotrygon* spp.)(top) and bluespotted fantail rays (*Taeniura lymma*)(bottom) in Bau Bau, Sulawesi, Indonesia in the late dry (left) and wet (right) seasons. Sightings were significantly higher in the wet season than both dry seasons, which were not statistically different from one another. Higher abundances of maskrays were observed in sandy habitat and higher abundances of fantail rays were observed at coral reef habitats.

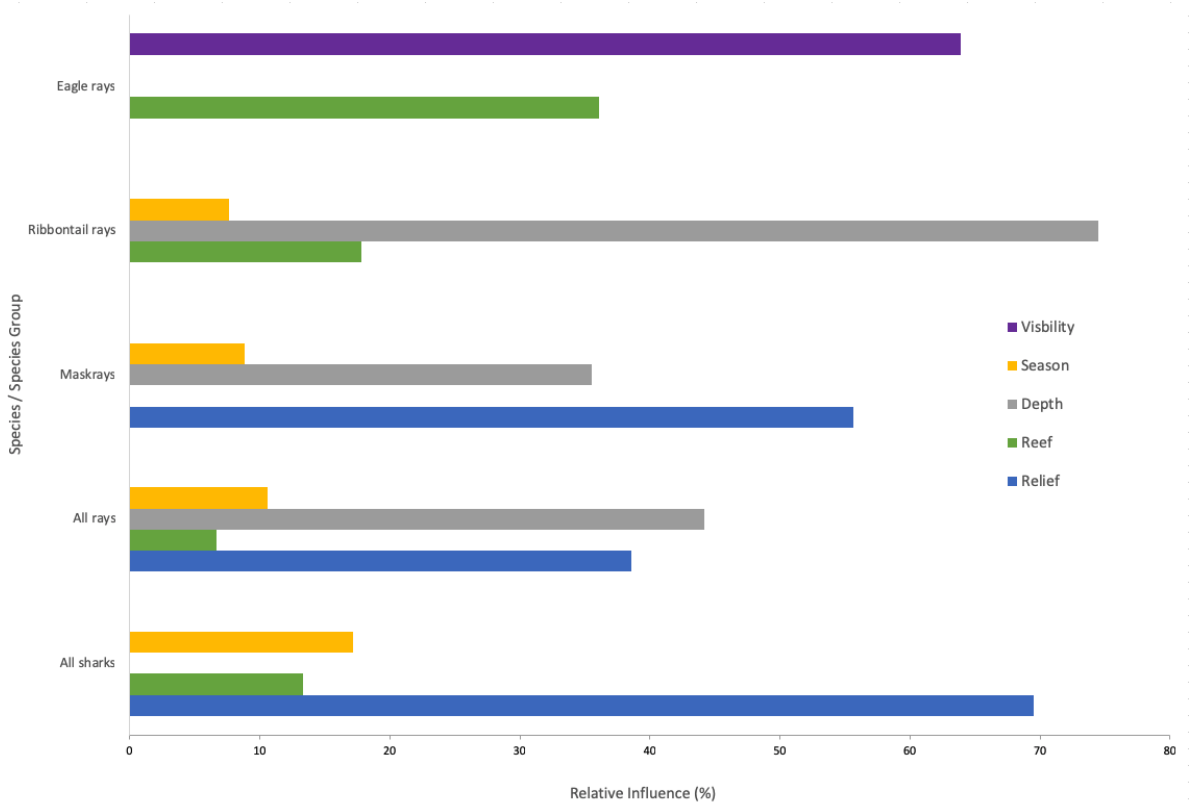


Figure 4.5. Relative influences of the explanatory variables for the different species / species groups based on generalized boosted regression models (GBM). Relief and depth were the two most important variables overall, while visibility was the most important variable in eagle ray abundance.

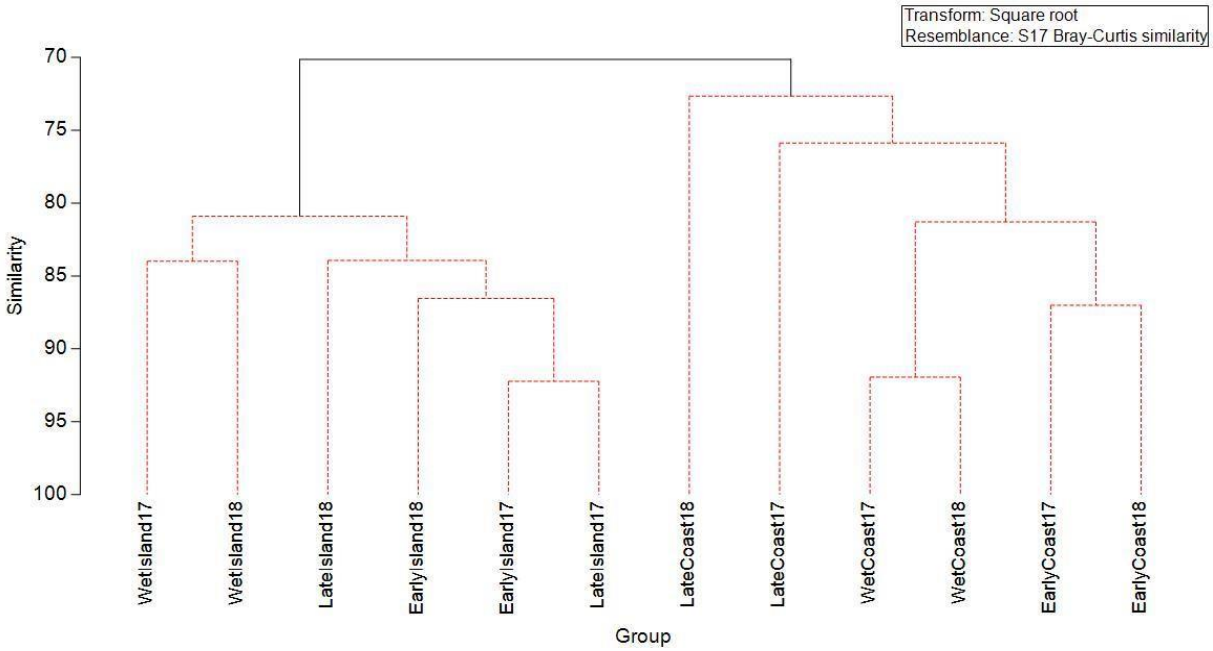


Figure 4.6. Cluster analysis using SIMPROF test where black lines indicate significant groups ($p<0.05$) and red dotted lines indicate anticipated groupings, but not at a significant level ($p>0.05$). The SIMPROF showed that the elasmobranch assemblage of the coast site was significantly different than that of the islands site. No other significant clusters were created.

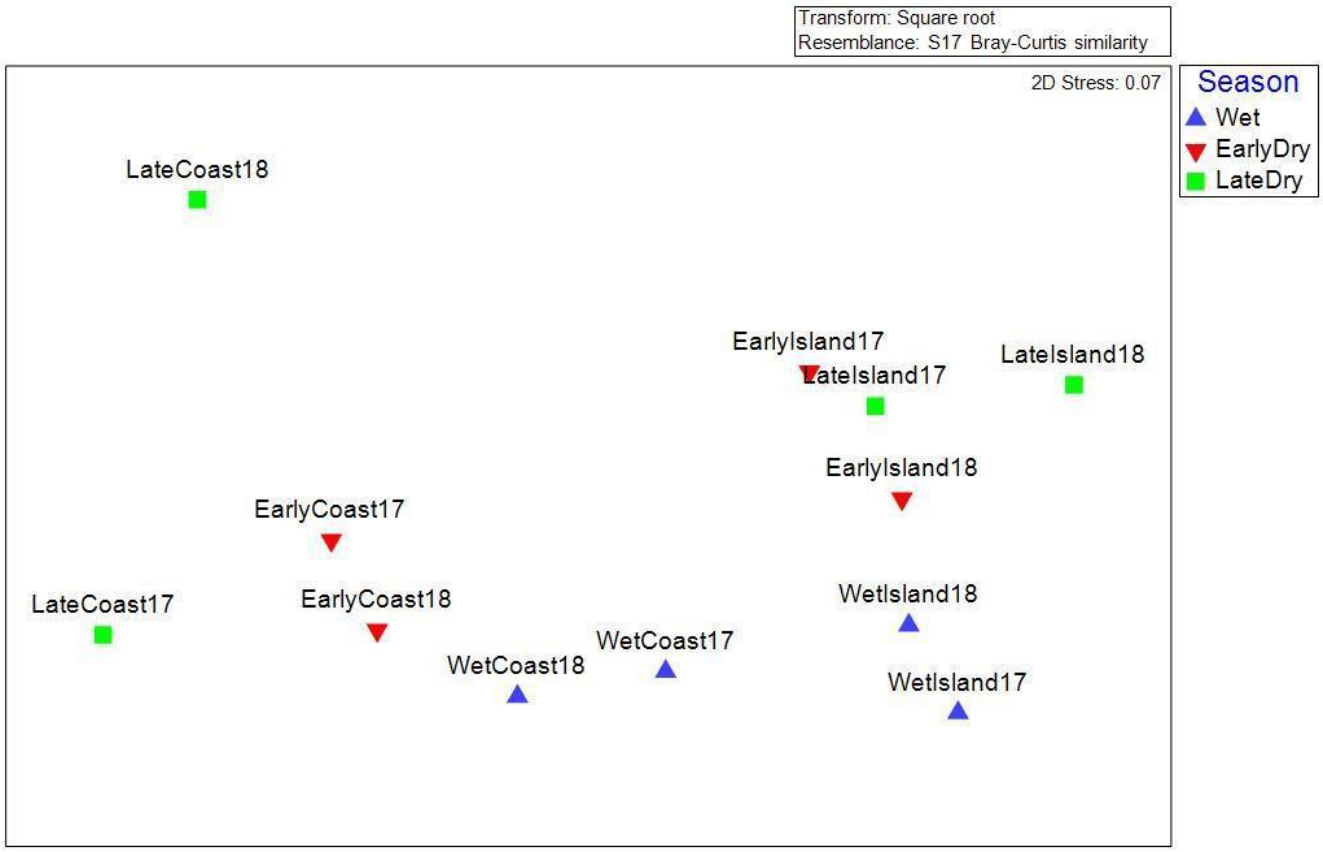


Figure 4.7. nMDS plot showing the separation of the islands site from the coast site. Additionally, wet season sampling periods form a loose cluster separate from the dry seasons.

Table 4.1. Possible species based on geographic range and similar appearance within the groups maskrays, eagle rays, and devil/manta rays.

Species Group	Common Name	Latin Name	Species Authority
Maskrays (*Neotrygon*)	Plain maskray	*Neotrygon annotata*	Last, 1987
	Australian bluespotted maskray	*Neotrygon australiae*	Last, White and Séret, 2016
	Bluespotted maskray	*Neotrygon caeruleopunctata*	Last, White and Séret, 2016
	Oriental bluespotted maskray	*Neotrygon orientalis*	Last, White and Séret, 2016
Eagle rays (*Aetobatus / Aetomylaeus*)	Mottled eagle ray	*Aetomylaeus maculatus*	Gray, 1834
	Banded eagle ray	*Aetomylaeus nichofii*	Bloch and Schneider, 1801
	Ornate eagle ray	*Aetomylaeus vespertilio*	Bleerker, 1852
	Longhead eagle ray	*Aetobatus flagellum*	Bloch and Schneider, 1801
	Spotted eagle ray	*Aetobatus ocellatus*	Kuhl, 1823
Devil / Manta rays (*Mobula*)	Reef manta ray	*Mobula alfredi*	Krefft, 1868
	Giant manta ray	*Mobula birostris*	Walbaum, 1792
	Kuhl's devilray	*Mobula kuhlii*	Müller and Henle, 1841
	Giant devilray	*Mobula mobular*	Bonnaterre, 1788
	Chilean devilray	*Mobula tarapacana*	Philippi, 1892
	Bentfin devilray	*Mobula thurstoni*	Lloyd, 1908

Table 4.2. Species and abundances of elasmobranchs observed on BRUVS in Bau Bau, South Sulawesi, Indonesia.

Common Name	Latin Name	Species Authority	Videos Present	Sum of MaxN
Bluespotted maskray complex	*Neotrygon* spp.	----------	250	369
Bluespotted fantail ray	*Taeniura lymma*	Forsskål, 1775	191	201
Eagle Rays	*Aetobatus / Aetomylaeus* spp.	----------	70	109
Coach whipray	*Himantura uarnak*	Gmelin, 1789	25	25
Pink whipray	*Pateobatis fai*	Jordan and Seale, 1906	32	57
Cowtail ray	*Pastinachus ater*	Annandale, 1909	7	7
Mangrove whipray	*Urogymnus granulatus*	Macleay, 1883	1	1
Porcupine whipray	*Urogymnus asperrimus*	Bloch and Schneider, 1801	2	2
Blotched fantail	*Taeniurops meyeni*	Müller and Henle, 1841	2	3
Bowmouth guitarfish	*Rhina ancylostoma*	Bloch and Schneider, 1801	1	1
Devil / Manta Ray	*Mobula* spp.	----------	3	3
Unknown Rays	----------	----------	5	6
Blacktip reef shark	*Carcharhinus melanopterus*	Quoy and Gaimard, 1824	272	316
Whitetip reef shark	*Triaenodon obesus*	Müller and Henle, 1837	38	38
Unknown Shark	----------	----------	2	2

Table 4.3. Results from MANOVA determining any temporal differences in abundance of all elasmobranch categories. Season was a significant factor in elasmobranch abundance.

Variable	Pillai's Trace	F	df	p
Year	0.01	1.74	6, 945	0.110
Season	0.06	4.46	12, 1892	<0.001
Year*Season	0.01	0.65	12, 1892	0.803

Table 4.4. Results of ANOVAs from the MANOVA test determining differences in species/ species group abundances at different temporal scales. All groups had significantly different abundances between the three seasons except for eagle rays and large stingrays. Eagle rays decreased significantly from 2017 to 2018 and this decrease was across all seasons. In no species/ species group was there any interaction of abundance between year and season. Significant results are bolded.

Species Group	Variable	Sum Squares	F	df	p
All sharks	Year	0.80	2.00	1, 950	0.158
	Season	**12.50**	**15.41**	**2, 950**	**<0.001**
	Year*Season	1.30	1.62	2, 950	0.198
All rays	Year	3.80	2.79	1, 950	0.095
	Season	**18.80**	**6.89**	**2, 950**	**0.001**
	Year*Season	0.70	0.27	2, 950	0.761
Maskrays	Year	1.00	1.58	1, 950	0.210
	Season	**5.30**	**3.99**	**2, 950**	**0.019**
	Year*Season	0.40	0.28	2, 950	0.755
Fantail ray	Year	0.00	0.01	1, 950	0.946
	Season	**1.25**	**3.31**	**2, 950**	**0.037**
	Year*Season	0.04	0.10	2, 950	0.908
Eagle rays	**Year**	**1.19**	**4.95**	**1, 950**	**0.026**
	Season	0.45	0.93	2, 950	0.395
	Year*Season	0.35	0.72	2, 950	0.486
Large stingrays	Year	0.10	0.43	1, 950	0.513
	Season	0.46	1.00	2, 950	0.368
	Year*Season	0.23	0.50	2, 950	0.608

Table 4.5. Top GLMM models for predicting SPUE (MaxN/hour) of the six species/species groups analysed. **'**ZINB' indicates zero-inflated negative binomial distribution and 'poisson' indicates poisson distribution. Difference between lowest corrected Akaike Information Criterion (ΔAICc), AIC weights (wAICc), and biggest VIF value of all variables in the model (Biggest VIF) are reported. Model selection was based on the most parsimonious model within two units of the lowest ΔAICc and with the biggest VIF value <5. Selected models are presented in bold. Variable codes: Relief – on a scale of 0-5 with increasing complexity, Season – wet or dry, Reef – coast or islands, Depth – in meters, Visibility – water visibility in 2 m bins (0-2, 2-4, 4-6, 6-8, 8-10, 10+).

Species Group	Model	ΔAIC	wAIC	Biggest VIF
All rays 'ZINB'	**Season + Reef + Relief + Depth**	**0**	**0.85**	**1.34**
	Season + Relief + Depth	3.54	0.15	1.18
	Relief + Depth + Reef	14.82	0	1.34
	Null	103.12	0	-
Maskrays 'ZINB'	**Season + Relief + Depth**	**0**	**0.50**	**1.79**
	Season + Relief + Reef + Depth	0.33	0.43	1.34
	Season + Reef*Relief	4.18	0.06	4.38
	Null	227.80	0	-
Fantail ray 'poisson'	Reef + Depth*Season	0	0.36	5.51
	Season + Reef + Depth	**0.70**	**0.25**	**1.00**
	Reef + Depth*Relief	1.09	0.21	4.40
	Null	65.13	0	-
Eagle rays 'poisson'	**Reef + Visibility**	**0**	**0.55**	**1.12**
	Reef + Season + Visibility	1.95	0.21	1.36
	Reef + Depth*Season	3.58	0.09	5.51
	Null	29.72	0	-
Large stingrays 'ZINB'	**Null**	**0**	**1**	**-**
	Reef*Relief + Season	23.09	0	4.38
	Reef*Relief	24.62	0	4.38
	UnconsolidatedHabitat	30.35	0	-
All sharks 'ZINB'	Season + Reef*Relief	0	0.93	4.38
	Season + Reef + Relief	**5.82**	**0.05**	**1.10**
	Season + Reef + Relief + Depth	7.82	0.02	1.34
	Null	114.98	0	-

Chapter 5

Distribution, Abundance, and Diversity of Rays in the Coral Triangle and Australasian Regions

Plate 5. Views from sampling across the Southeast Asia (top = Nguna, Vanuatu; centre left = Boheydulong, Malaysia; centre right = Kuroshima, Japan; bottom = Bau Bau, Indonesia).

5.1 Introduction

Coral reef ecosystems are highly dynamic environments with complex trophic interactions and environmental drivers (Opitz 1996; Nyström and Folke 2001). Some of these ecosystems are heavily impacted by human activity due to their high economic value (Spurgeon 1992; Chin et al. 2011). Anthropogenic impacts have stretched to even the most remote reefs as fishing technology and food storage improves (Torres-Irineo et al. 2014; Tickler et al. 2018). Therefore, the presence of pristine coral reefs remains questionable in the Anthropocene and its definition nearly impossible. Well-enforced marine protected areas (MPAs), both no-take and partially protected, have higher abundances of upper trophic level species, like sharks, than adjacent unprotected waters (Davidson and Dulvy 2017), suggesting high abundances of predators may be good indicator for a healthy reef. It has also been shown that shark abundances increase with distance from human populations, suggesting high anthropogenic impacts on top predator abundances (Ward-Paige et al. 2010; Nadon et al. 2012). Due to ease of access and livelihood dependence, areas with large human populations are often heavily targeted by fishing (Cinner et al. 2018) and predator populations are often heavily depleted in these regions. Until now, however, rays have been understudied in coral reef ecosystems compared to their relatives the sharks.

Rays are a diverse group of species with pelagic, epipelagic, or benthic lifestyles, planktivores or active hunters, and small to large bodied individuals (Kriwet et al. 2009; Last et al. 2016). Many species of rays are found in coral reef ecosystems including small to large stingrays (family: Dasyatidae), pelagic rays like eagle rays (family: Myliobatidae) and mobulids (family: Mobulidae), as well as shark-like rays (family: Rhinidae)(Last et al. 2016). Rays have several important ecological roles in coral reef ecosystems (Laverock et al. 2011;

Couturier et al. 2013; Ajemian and Powers 2014; Martins et al. 2018). They act as important bioturbators, increasing nitrogen fixing and oxygen levels within sediments, which provides habitat for benthic infauna (Laverock et al. 2011; O'Shea et al. 2012). Through migration and daily movements, rays link ecosystems. For example, reef manta rays (*Mobula alfredi*) are capable of diving to depths greater than 400 m to feed on deep-water plankton (Braun et al. 2014; Peel et al. 2019). After these dives, they return to surface waters to heat up, bringing nutrients back to shallower ecosystems, including reefs (Braun et al. 2014). Similarly, some species link ecosystems with seasonal migrations, like the cownose ray (*Rhinoptera bonasus*), which exhibits periodic residency in small areas and large-scale movements seasonally (Collins et al. 2007). Coral reefs are species rich ecosystems and have many species to fulfil all ecological niches for ecosystem function, with some functional redundancy (Loreau 1998; Bellwood et al. 2003). Given the limited research on rays and their ecological roles on coral reefs, it is hard to predict the consequences of losing these species.

Rays as a group are heavily fished, particularly in developing countries like those in Southeast Asia (Dulvy et al. 2017). Rays comprise five of the seven most endangered elasmobranch families with 20% of ray species listed in a threatened category by IUCN and a further 25% listed as data deficient (Dulvy et al. 2014). Fishing is the single greatest threat to ray populations, as they are both targeted and caught incidentally in many fisheries (Bonfil 1994; Stevens et al. 2000; Davidson et al. 2016). However, climate change, habitat loss and pollution also contribute to population declines (Chin et al. 2010; Gelsleichter and Walker 2010; Dulvy et al. 2016). Most elasmobranchs are susceptible to over-exploitation due to their life history characteristics of low fecundity, slow growth, and late age of maturity (Camhi et al. 1998; Cortes et al. 2010). The consequences of fishing pressure on rays is often

overshadowed by the large amount of attention from researchers and the media focused on sharks and shark fishing. However, ray landings reported to FAO are greater than shark landings (White and Dharmadi 2007; Dulvy et al. 2014). Rays are used for their meat, leather and gill plates (Grey et al. 2006; Mardiah et al. 2012). Southeast Asia is a global biodiversity hotspot for coral reef species, including rays and sharks (Allen 2008; Tittensor et al. 2010). It is also home to many of the largest elasmobranch fishing nations and has the highest level of threatened elasmobranch species (White and Dharmadi 2007; Dulvy et al. 2017). Population abundances of rays often respond quickly to changes in fishing pressure, recovering when fishing pressure is decreased (Garofalo et al. 2003). Rays have also been shown to respond to changes in predator abundances, increasing in abundance when predators are reduced or removed from the ecosystem (Valinassab et al. 2006).

The aims of this study were to determine the assemblage of rays and their abundances across ten countries in the Coral Triangle and Australasian regions: Australia, Indonesia, Japan, Malaysia, Papua New Guinea, Philippines, Solomon Islands, Taiwan, Vanuatu, and Vietnam. Additionally, I examined the drivers of ray abundances, both natural and anthropogenic. I hypothesized that countries with lower fishing pressure would have moderate abundances of rays due to predation risk from sharks (see Chapter 6), which are more abundant in lightly fished reefs, but have higher ray species richness due to the low fishing pressure. In heavily fished reefs, higher abundances of rays were expected due to their higher productivity and lower predation risk, as sharks would be removed. Similarly, ray assemblage was expected to be similar in countries with similar levels of fishing pressure (**Table 5.1**). Due to their association with the benthos, habitat variables such as benthic relief and benthic cover were expected to be the natural drivers of ray abundance.

5.2 Methods

5.2.1 Study Sites

Seventy reefs within 39 sites in 11 countries were sampled with baited remote underwater video systems (BRUVS) between October 2015 and August 2018 using a stratified random sampling design (***Appendix I***). Australia was split into the Indian Ocean and Pacific Ocean, each called a separate 'country' for analytical purposes. Given the aim of this study was looking at the impacts of fisheries management on ray abundance and diversity and fisheries management in Australia that would affect coral reefs is under jurisdiction of each state, this split was warranted.

5.2.2 Sampling

A total of 3426 BRUVS were deployed at 70 reefs with up to seven units deployed at once during daylight hours. BRUVS were deployed a minimum of 500 m apart at 0.5 m to 70 m depth in coral reef habitats with an average depth of 15.92 ± 0.15 m. BRUVS were left for a minimum of 60 mins however due to battery life, some deployments did not reach the 60-minute mark. All deployments that were a minimum of 30 minutes were used in analyses. Deployments spanned across a variety of habitat types including reef crest, forereef, adjacent seagrass, lagoon, and sand flats. Up to 28 BRUVS were deployed per day. Two types of BRUVS were used in this study. The first consisted of aluminium frames that housed a GoPro Hero 4 Silver camera with wide angle view (approx. 170° in air), (1920 X 1080 video format, 30 frames/s) housed in NiMAR housings. The second type was a stereo set-up consisting of an aluminium frame with two GoPro Hero 4 Silver cameras in custom housings with medium angle view (approx. 120° in air), (1920 x 1080 video format, 30 frames/s). In both set-ups a bait arm extended 1 m from the camera containing 1 kg of the oiliest fish available in each location. In decreasing order, bait used was crushed pilchards

(*Sardinella* spp.), slimy mackerel (*Scomber australiasicus*), tuna (*Thunnus* spp.), fusilier (*Caesio* spp.), wahoo (*Acanthocybium solandri*), and coral trout (*Plectropomus leopardus*).

5.2.3 Video annotation

BRUVS footage was analysed according to Chapter 4.2 for MaxN of all elasmobranch species using either Event Measure software (www.seagis.com v.4.43) or FinPrint Annotator (v.1.1.44.0). All videos were read by two independent annotators and species identification was validated by a senior reviewer.

5.2.4 Environmental Information

Environmental factors noted at the time of deployment included: date, time, location (latitude/longitude), depth (m), and wind speed (Beaufort scale). Deployment times were split into morning (sets deployed before 10:29), midday (sets deployed from 10:30-13:29) and afternoon (sets deployed after 13:30). Visibility, habitat and relief were analysed using BenthoBox software (www.benthobox.com). Visibility was determined using 2 m groupings (0-2, 2-4, 4-6, 6-8, 8-10, and 10+ m). Relief was analysed using a 20 square grid on top of an image from the deployment. Each square within the grid containing benthos was given a relief score from 0 (flat) to 5 (complex) and the average relief for each deployment was calculated. Habitat was also analysed using a 20 square grid. For each square, the majority habitat category was selected and percent cover was calculated based on the total number of squares containing benthos. Possible benthos categories were hard coral, soft coral, bleached coral, unconsolidated (sand/rubble), consolidated (rock), seagrass, turf algae, macroalgae, sponge, true anemones, ascidians, crinoids, halimeda, hydrocoral, hydroids, and invertebrate complex. A ratio of live coral to other substrate was also calculated for habitat analyses using percent cover obtained from BenthoBox. 'Human gravity' was

calculated per BRUVS deployment as intensity of human impact based on population size, reef protection status, and reef accessibility (Cinner et al. 2018). Reef protection status was also included as either protected (no-take MPA), restricted (fishing allowed with restrictions either size, bag limits, temporal, etc.), and open (no fishing restrictions for elasmobranchs).

5.2.5 Species

Up to 33 species from 12 genera and six families were observed. However, exact species details cannot be confirmed because species identification was not always possible. Thus, all eagle rays (Genera: *Aetobatus and Aetomylaeus*) were grouped as one, all maskrays (Genus: *Neotrygon*) were grouped, all manta and devil rays (Genus: *Mobula*) were grouped, and all wedgefish (Genus: *Rhynchobatus*) were grouped (**Table 5.1**). Additionally, only a single individual of the Oceanic fantail ray (*Taeniura lessoni*) was observed, therefore, this was included with the similar species, the bluespotted fantail ray (*T. lymma*) to be the fantail ray group (Genus: *Taeniura*). These were grouped together as their ranges do not overlap but they are similar in size, behaviour, and ecosystem function (Last et al. 2016). The number of species of sharks from each country was also calculated. In some cases individuals were not able to be identified to species and were not included for the species count.

Nine species of large benthic stingrays with maximum disc widths greater than 1 m were observed in low abundances (*Himantura australis, H. leoparda, H. uarnak, Pastinachus ater, Pateobatis fai, P. jenkinsii, Taeniurops meyeni, Urogymnus asperrimus,* and *U. granulatus*). Due to the low sample size and similar ecological niches, these species were combined for analyses and called the “large stingray” group.

5.2.6 Statistical Analyses

Sightings per unit effort (SPUE) was calculated by dividing the MaxN of all ray species observed in a deployment over the total length (hours) of the deployment to obtain a value of rays per hour. The SPUEs from each deployment were then averaged for each reef, site and country. Using R (version 3.5.1) generalised linear mixed models (GLMM) were performed (R package – lme4 (Bates et al. 2019)). GLMMs were run with Poisson distributions and a zero-inflation factor of 1. The variables of reef nested in site were included as random effects variables. Thirty-five ecologically relevant models and a null model were tested with the dependent variable of SPUE and each of the three most commonly observed genera independently (maskrays (*Neotrygon* spp.), fantail rays (*Taeniura* spp.), and eagle rays (*Aetobatus / Aetomylaeus* spp.)); and the grouping of large stingrays. The most parsimonious model with an AIC value within two units of the lowest AIC value was chosen as the final model. Model variables were tested for collinearity using variance inflation factors (VIF). Only models where the highest VIF value was <5 were considered (Akinwande et al. 2015). To examine differences between ray abundances in each country and time of day, a one-way ANOVA was used. Tukey HSD post-hoc tests were performed to determine where differences in SPUE occurred. A simple linear regression was performed comparing ray species richness to shark species richness at the country level.

Community analyses were performed in PRIMER (version 7). Ray abundances for each species / species group at each reef were square root transformed to reduce the leverage of the most commonly observed species. A one-way SIMPER was run using a Bray-Curtis similarity with country as the factor. Dissimilarity distances were calculated using a Bray-Curtis similarity. A two-way nested ANOSIM was run where ‘site’ was nested within

'country.' Spearman ranks were used as the correlation method with 4,999 permutations run. Similarity profile tests (SIMPROF) were used to determine whether similarities observed between countries and sites with the CLUSTER analyses were significant or by chance. The test was performed using Bray-Curtis similarity matrix and groupings were examined at $p < 0.05$ with a maximum of 4,999 permutations. A non-metric multidimensional scaling (nMDS) plot was created analysing all sites at which rays were present, using 50 restarts and a minimum stress of 0.1.

5.3 Results

5.3.1 Deployments

In 3426 BRUVS deployments, 1069 individuals of up to 33 species from 12 genera and six families of rays were observed (**Table 5.2** and **5.3**). The most abundant rays were the maskrays, fantail rays, and eagle rays with 330, 328, and 194 individuals, respectively. 145 individuals from the large stingray group were observed (~45% of which were pink whiprays, *Pateobatis fai*). Only a single individual of three species were observed, one porcupine ray (*Urogymnus asperrimus*) was seen at Heron/Wistari Yellow Zone in Australia, one ringed guitarfish (*Rhinobatos hynnicephalus*) was seen at Penghu North in Taiwan and one reticulate whipray (*Himantura australis*) was seen at Townsville Site 1 in Australia. The leopard whipray (*Himantura leoparda*) was not confirmed on any BRUVS in this study, however, it was suspected for an individual that was counted as an 'unknown ray.' Therefore, it is included in the species list for this study.

There were significant differences in the SPUE of rays between the 11 countries ($F = 21.63$, $df = 10, 3414$, $p<0.001$)(**Fig. 5.1** and **5.2**). A Tukey HSD post-hoc test showed Indonesia had significantly higher SPUE of rays than all other countries at 0.545 ± 0.035 rays/hour (**Fig.**

5.2 and **Table 5.4**). Vietnam had the lowest SPUE at 0.004 ± 0.004 rays/hour. Australia – Pacific Ocean and Indonesia had the highest diversity with 10 different species / species groups present, while Vietnam only had one individual observed (**Fig. 5.1** and **5.2**).

5.3.2 Ray Assemblage

There were significant differences in species composition among sites and countries (Two way nested ANOSIM, R statistic: site- 0.271, country- 0.264, both permutations – 4,999, p-value: site – 0.004, country – 0.003). Indonesia, Malaysia, the Philippines, Taiwan, and Vietnam all had significantly different species composition than at least four other countries. Japan and the Solomon Islands were only significantly different from one country, Indonesia (***Appendix II***). The three most abundant genera were the highest contributors to differences both between and within countries. Devil rays and manta rays (*Mobula* spp.) contributed to species composition difference between Japan and four other countries, likely due to sightings of *Mobula* spp. in Japan and few sightings in other countries. Other species that contributed to differences between countries included pink whiprays (*Pateobatus fai*), and blotched fantail rays (*Taeniurops meyeni*)(***Appendix II***).

Vietnam and the Solomon Islands species compositions were significantly different from each other and to the other nine countries (**Fig. 5.3**). The analysis also significantly separated Australia (Pacific and Indian Ocean sites), Indonesia, Malaysia, and Papua New Guinea into one grouping (Group 1; higher species richness, including diverse larger bodied ray species) and Japan, Philippines, Taiwan, and Vanuatu in another grouping (Group 2; mainly consisting of maskrays and eagle rays (**Fig. 5.1** and **Fig. 5.3**). Taiwan significantly split from Group 2, likely due to the endemic species observed there (ringed guitarfish - *Rhinobatus hynnicephalus*) and the higher abundance of blotched fantail rays (**Fig. 5.3**).

There were few distinct groupings at the site level. Cobourg, in Australia was significantly distinct from all other sites. Additionally, three sites in Taiwan (Green Island, Orchid Island, and Penghu) were significantly distinct and grouped away from all other sites. While several other site groupings were formed, no significant clusters were created (**Fig. 5.4**).

Non-metric multidimensional scaling (nMDS) showed a similar cluster of the Taiwan sites as the SIMPROF. Additionally, the plot shows the three Great Barrier Reef sites in close proximity to one another and close to Indonesia, Malaysia, and Papua New Guinea sites (**Fig. 5.4**). Ray species richness was significantly positively related with shark species richness as shown by a simple linear regression ($F = 7.02$, $df = 1,9$, $p = 0.026$)(**Fig. 5.5**).

5.3.3 Drivers of Ray Abundances

Ray (all species) abundance (SPUE) was significantly influenced by country, benthic relief and the time of day (**Table 5.5**). Overall SPUE decreased significantly with increasing relief (**Fig. 5.6a**). Ray SPUE increased throughout the day, however this increase was not significant (ANOVA: $F = 2.42$, $p = 0.089$; Tukey: all groups $p>0.05$)(**Fig. 5.7**).

Four groups of species (maskrays, fantail rays, eagle rays, and large stingrays) were found in higher abundances and in at least seven of the ten countries included in this analysis, allowing for further species-specific analyses. Eagle rays were found in all countries in this study, maskrays were found in all countries except the Solomon Islands and Vietnam, and fantail rays were found in all countries except Japan, the Philippines, and Vietnam (**Fig. 5.1**). At least one species from the large stingray group was found in each country except for Vietnam. The most widely dispersed large stingray was blotched stingrays (*Taeniurops meyeni*), which were found in nine countries (all except the Solomon Islands and

Vietnam)(**Fig. 5.1**).

The best models for maskray, fantail ray and large stingray abundance included country and relief (**Table 5.5**). For maskrays, like rays overall, time of day was also a significant contributor to abundance. In maskrays, significantly more individuals were observed in the afternoon than morning as shown by an ANOVA and Tukey post-hoc test (ANOVA: $F = 5.40$, $p = 0.005$; Tukey: Morning-Midday $p = 0.385$, Midday-Afternoon $p = 0.081$, Morning-Afternoon $p = 0.003$)(**Fig. 5.7**). Fantail ray abundance significantly decreased with increasing depth and decreasing relief (**Fig. 5.6b** and **5.6c**). Eagle ray abundance was explained by percent cover of unconsolidated habitat such that their abundances increased with increasing cover (**Table 5.5** and **Fig. 5.6d**). Large stingrays were significantly influenced by country and relief. Large stingray abundance decreased with increasing relief (**Fig. 5.6e**).

5.4 Discussion

This study is one of the first to describe ray assemblages in coral reef ecosystems and does so over a large geographic range. In the Indo-Pacific region, there has been an abundance of research on the shark assemblage (Espinoza et al. 2014; Papastamatiou et al. 2018), however, similar work on rays is lacking, despite the diversity of species and ecological roles they perform (Chapter 2). Ray assemblage composition was relatively conserved throughout the region, with a consistent core group of species that included maskrays (*Neotrygon*), fantail rays (*Taeniura*), eagle rays (*Aetobatus* and *Aetomylaeus*), and a small number of large stingrays. The abundance of rays in the Coral Triangle and Australasian regions, however, was highly variable, driven by a range of factors including biogeography, different habitats, and human influence. Although ray assemblage was similar, higher ray richness was not correlated with higher ray abundance. Countries with higher shark species

richness did have higher ray species richness, although the drivers of this relationship could not be determined.

High species richness has been suggested as an indicator of resilient reefs with high functional redundancy (Connell 1978). Thus, a reef with higher ray richness may be indicative of a more resilient reef as more ecological niches are occupied. Functional extinction, where there are too few individuals to perform their ecological role, can severely impact ecosystems (Sellman et al. 2016). This has been observed in elasmobranchs like sawfish in the Gulf of Oman (Moore 2015). However, there is little research on this topic for elasmobranchs. Examples from other taxa show large impacts on coral reefs from functional extinctions including the loss of rabbitfish in the Caribbean leading to phase shifts due supressed herbivory (Bellwood and Goatley 2017), and the reduction in coralline algae in Fiji where predatory teleosts were fished to functional extinction (Dulvy et al. 2004). Due to the relationship between ray species richness and shark species richness, improved management for one group would likely benefit the other as well. In order to reach conservation goals, one group can be used as an "umbrella group" to protect the other. With the current level of research on sharks, there is a plethora of evidence that many populations are declining (Robbins et al. 2006; Bradley et al. 2017; Hammerschlag et al. 2018). Compared to the paucity of data on rays and the lack of charisma associated with the group (with the exception of manta rays), shark declines provide compelling arguments to promote shark conservation. This could lead to protection and regulations that would benefit rays.

Species with longer generation times, like larger sharks and rays, are more susceptible to overfishing due to their low productivity (Frisk et al. 2001). This has been observed in

markets in heavily fished areas where smaller, more productive species and individuals are more commonly sold compared to historic species and size classes (To and Sadovy de Mitcheson 2009). With low levels of fishing pressure, higher richness and abundances of larger species of elasmobranchs would be expected, as was observed in the Solomon Islands and Vanuatu with sharks (unpublished data)(**Table 5.1** and **Fig. 5.8**). As fishing pressure increases, predation rates on rays would decrease due to the reduced abundances of sharks which are more commonly targeted than rays. The richness of larger species would likely remain, however, abundances would begin to decrease. This was observed in Papua New Guinea and Taiwan with high ray species richness but moderate SPUE. Taiwan had relatively high ray richness, including one endemic species (ringed guitarfish, *Rhinobatos hynnicephalus*). This may be a successful result from an extensive effort made in the late 1990s to early 2000s to reduce fishing capacity (Huang and Chuang 2010), which likely had a positive impact on the ray community. With further fishing pressure increases, often coinciding with poor management, low compliance and reduced shark predation, more productive ray species would dominate the elasmobranch community and top predators would be absent, as observed in Indonesia and Malaysia (**Fig. 5.8**). Finally, once fishing pressure reaches a threshold in which even productive species are removed faster than they can reproduce, there would be a collapse and almost complete absence of mesopredators. This was seen in Vietnam, which has intense near-shore fisheries due to ease of access and suitability for trawling (Pomeroy et al. 2009). This shows the level of fishing pressure on coral reef ecosystems significantly affects the elasmobranch community as rays are influenced by both fishing pressure and shark abundances.

An increasingly common conservation tool in fisheries management are Marine Protected Areas (MPAs)(Christie et al. 2002). Well enforced MPAs in coral reef habitats have proven

to have higher fish biomass and shark presence (Bond et al. 2012; Espinoza et al. 2014), leading to the assumption that they are healthier ecosystems than fished areas nearby. MPAs are also increasingly being used in developing countries as a relatively easy solution to reduce fishing pressure (Sario 2016). Despite deploying BRUVS within MPAs of each country, protection status was not a significant predictor of ray abundance or richness. MPAs must be well-enforced to provide the positive results they were put in place to generate (Rife et al. 2012). The lack of response by rays to protection status either indicates a lack of compliance, that MPAs are not a viable conservation strategy for rays, or a combination of the two. Considering the low levels of enforcement in most countries examined (**Table 5.1**), many MPAs were likely only "paper parks", meaning although legislation has been put in place, there is minimal enforcement and thus often low compliance, therefore, no actual protection (Thur 2010; Rife et al. 2012)(**Table 5.1**). In Malaysia, one site (Sipadan) is a well-managed and enforced MPA less than 20 km, but isolated by depth from the openly fished Mabul site, which frequently has trawlers within 500 m of the island (pers. obs). At Sipadan, no rays were observed in this study but there were many sharks whereas the opposite was found in Mabul. Similar results of higher shark abundances within MPAs have been observed globally (Ward-Paige and Worm 2017), particularly those MPAs that are no take, well enforced, old, large, and isolated (Edgar et al. 2014). Sipadan is four of those five characteristics as it is a small island. The absence of rays but high abundances of sharks at Sipadan, and high shark abundances in other MPAs globally shows their effectiveness for some elasmobranchs, but not necessarily for rays. A similar result was observed for shark-like rays in Australia, where no correlation was found between abundance and area protection status (White et al. 2013). In this study, the Philippines overall had high richness of rays and a low SPUE. One site, Tubbutaha, contributed to the high richness and most of the ray abundance in the country. This site is also a well-enforcement MPA. Other locations

in the Philippines have poor enforcement levels (Green et al. 2003) and had low ray richness and SPUE, which contradicts what was observed in Malaysia. However, Malaysia had higher abundances of sharks than the Philippines, so it is possible that MPAs are effective for the top predators in an ecosystem. In the Philippines, where sharks have been mostly removed, rays would be amongst the upper trophic level species (**Fig 5.8**). Therefore, MPAs in regions with lower abundances of top predators may have positive effects on mesopredators, including rays. With continued protection and low fishing pressure, sharks may reappear in these protected areas, moving them back to a more natural elasmobranch community (**Fig. 5.8**). The inconsistent results from MPAs in this study show the magnitude and variability that full protection and enforcement can have on the ray community on coral reefs. As rays respond to fishing pressure and shark abundances both directly through predation, and indirectly through changing behaviour in areas with higher shark abundances, further research is required to understand the complex dynamics of MPA effects on ray populations in areas with varying shark abundances.

Indonesia and Malaysia had the highest relative abundance of rays. These two countries have also been among the top 10 elasmobranch catching nations since 1980 (Lack and Sant 2009; Dulvy et al. 2017)(**Table 5.1**). Few sharks were observed on BRUVS in these locations, however, the abundance of rays points to possible mesopredator release caused by overfishing of their main predators (i.e. sharks)(Ferretti et al. 2010). In the Persian Gulf and Oman Sea, there were increases in ray abundances following decreases in shark populations (Valinassab et al. 2006). This may be due to mesopredator release, which results in increases in mesopredator abundances or behavioural shifts by the rays compared to areas of low predator abundance (see Chapter 6). Although 10 species of rays were observed in Indonesia, there were less than 10 individuals from all species except three, despite

extensive sampling. Two of those were small, productive species and one pelagic species less likely to be caught by most fishers. This means although the ray community is rich, it is dominated by the two smaller genera (maskrays and fantail rays). With many species being absent or having reduced abundances, some ecological roles may not be filled, meaning some important ecosystem processes may not occur.

Life history and productivity of species will significantly affect their susceptibility to overfishing and recovery time of depleted stocks (Adams 1980). For rays, productivity and generation times are related to body size (Frisk et al. 2001). Therefore, the abundance of smaller ray species in countries with high fishing pressure and, thus, low shark abundance was expected as these rays would be prey to sharks that live on reefs (**Table 5.1**). Similarly, due to higher productivity, small rays would also be less affected by fishing pressure than larger rays. Larger rays were mostly absent from heavily fished reefs which confirms their susceptibility to fishing pressure as their generation times are longer than those of smaller rays, correlating to lower lifetime fecundity (Frisk et al. 2001). Larger rays are frequent bycatch in longlines (Piovano et al. 2010), trawls (Buxton et al. 1984; Clarke et al. 2016), and gillnets (Trent et al. 1997; Moazzam and Nawaz 2014). Thus, the reduced abundance of large rays in countries with higher fishing pressure is likely a result of bycatch in fisheries in conjunction with lower lifetime fecundity of larger rays (**Fig. 5.8**). Differing life history characteristics and susceptibility of ray species stresses the importance of species-specific fisheries management for rays.

Habitat quality and characteristics also affect the ray community at finer scales than fishing pressure. Benthic relief was the most important variable for predicting ray abundances and was included in the top model for all species / species groups, with the exception of the

eagle rays, which were influenced by the percentage of unconsolidated cover (which was directly correlated to relief). As rays are benthic animals, they are strongly associated with certain benthic habitats. Maskrays were found in significantly higher abundances in low relief habitats as they both feed and shelter in sand (Last et al. 2016). Fantail rays were more abundant in higher relief habitats, such as coral reefs, as they hide under corals rather than bury in sand (Dabruzzi et al. 2013). Anthropogenic impacts like climate change and destructive fishing practices are an increasing threat to coral cover and coral reef structure (McManus et al. 1997; Hoegh-Guldberg et al. 2017), which may negatively impact certain ray species, like fantail rays, more than those that do not directly rely on coral structure, like maskrays.

Rays (all species) and maskrays were influenced by time of day, such that there were increasing abundances from morning to afternoon. The increased sightings of rays in the afternoon may be due to increased activity levels and predator avoidance. Reef predators tend to be more active and forage in the early morning and evening (Bosiger and McCormick 2014; Papastamatiou et al. 2015). Additionally, as small ectotherms, diel temperature variation may play a role in the activity level of rays such that they are more active as the water warms throughout the day (Higgins 2019). Changes in activity levels and likelihood of observation should be considered in sampling design for these species.

This study provided insight into the ray community in the Coral Triangle and Australasian regions. Rays in these areas are clearly affected by a range of factors, most notably fishing and habitat suitability. In order to conserve rays and their ecosystem services, fisheries management must be addressed and better implemented. Through fisheries management, other important species like sharks and other large predators would also benefit. While

there is a large amount of work on shark abundances globally, similar work on rays is lacking. This, of course, hinders our understanding of the ecological role and importance of rays, which hinders understanding human impacts on them. Without knowing the full extent of human impacts on rays, it is difficult to determine where and how much conservation effort is required. With reefs under anthropogenic pressure from fishing, coastal development, and climate change, there are also impacts to ray habitats in addition to fishing pressure. These must be addressed in a holistic approach prioritising fishing mortality, then habitat protection.

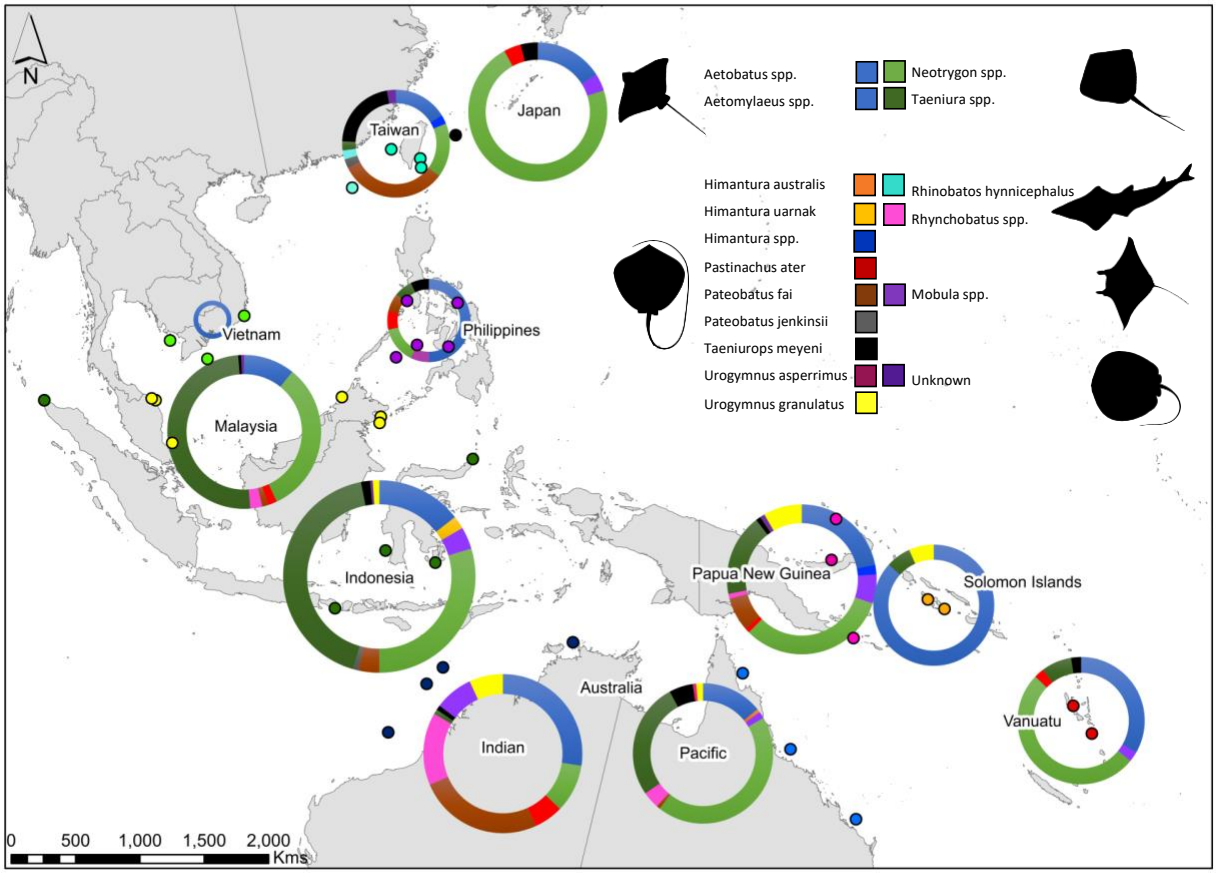


Figure 5.1. Map of all sites sampled in this study. Ring graphs indicate species composition of each country and size of the ring graphs is cube root proportional to SPUE of rays. Sites are colour coded so that all sites within a country have the same colour dots [Australia (Indian Ocean) – navy blue, Australia (Pacific Ocean) – blue, Indonesia – dark green, Japan – black, Malaysia – yellow, Papua New Guinea – pink, Philippines – purple, Solomon Islands – orange, Taiwan – turquoise, Vanuatu – red, Vietnam – light green].

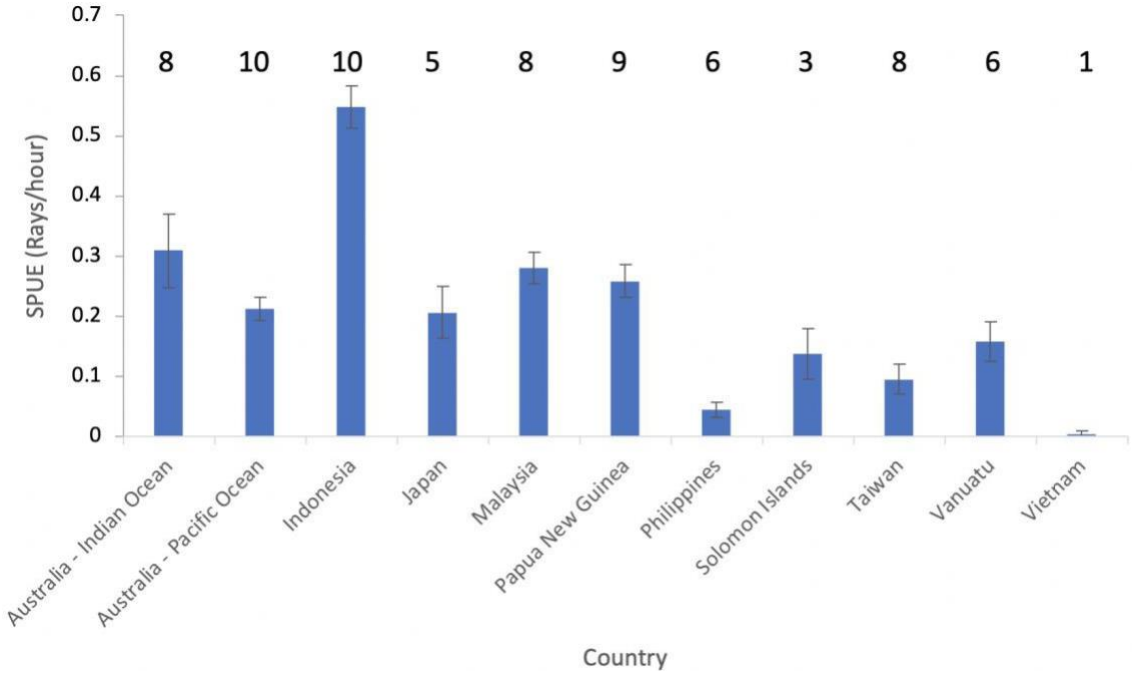


Figure 5.2. Mean sightings per unit effort (rays/hour) ± SE of the 11 countries included in this study. Numbers above bars indicate number of different species / species groups observed in each country. Indonesia had a significantly higher SPUE, as shown by a Tukey HSD post-hoc test, than all other countries included in this study.

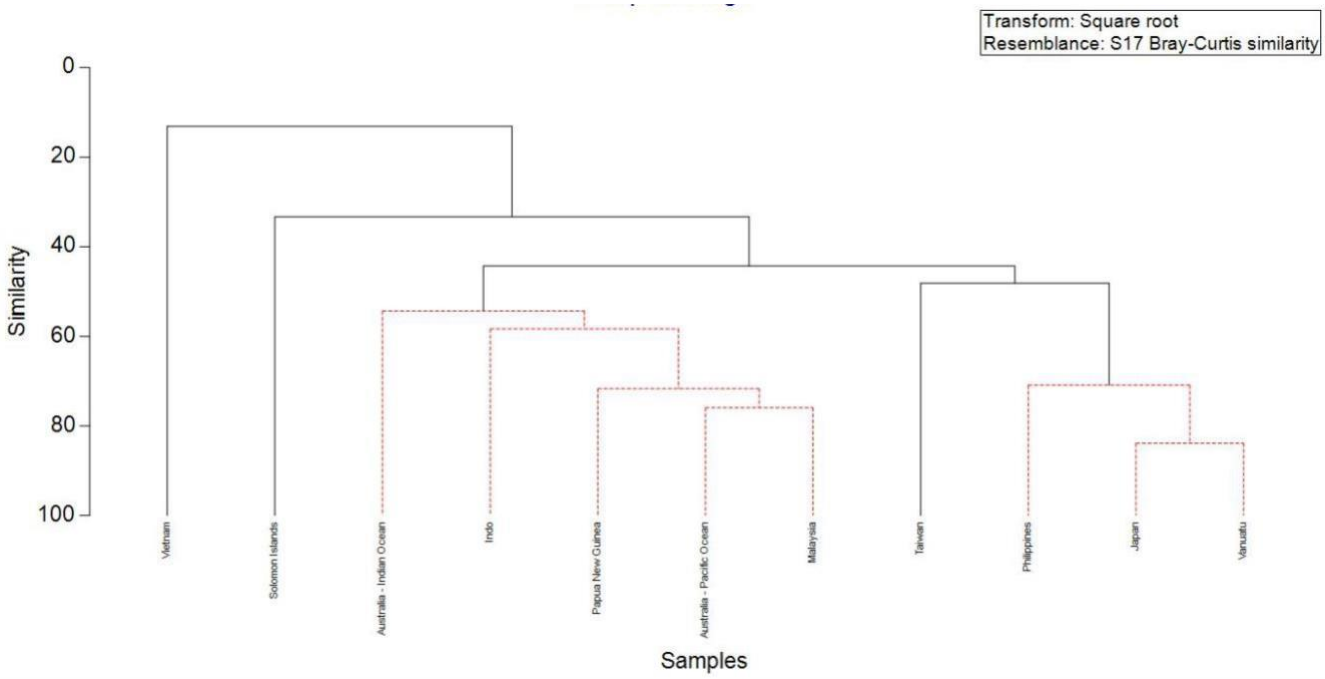


Figure 5.3. Cluster analysis using SIMPROF test to determine groupings of countries. Solid lines indicate significant distinctions in groups ($p < 0.05$), red dotted lines indicate anticipated groupings, but not at a significant level. Vietnam and the Solomon Islands are significantly distinct from each other and the other countries with similarity <40%. Two distinct groups emerged: Group 1 – Australia, Indonesia, Malaysia, and Papua New Guinea, which had higher species diversity and Group 2 – Japan, Philippines, Taiwan, and Vanuatu, in which mostly maskrays and eagle rays were observed with few other species.

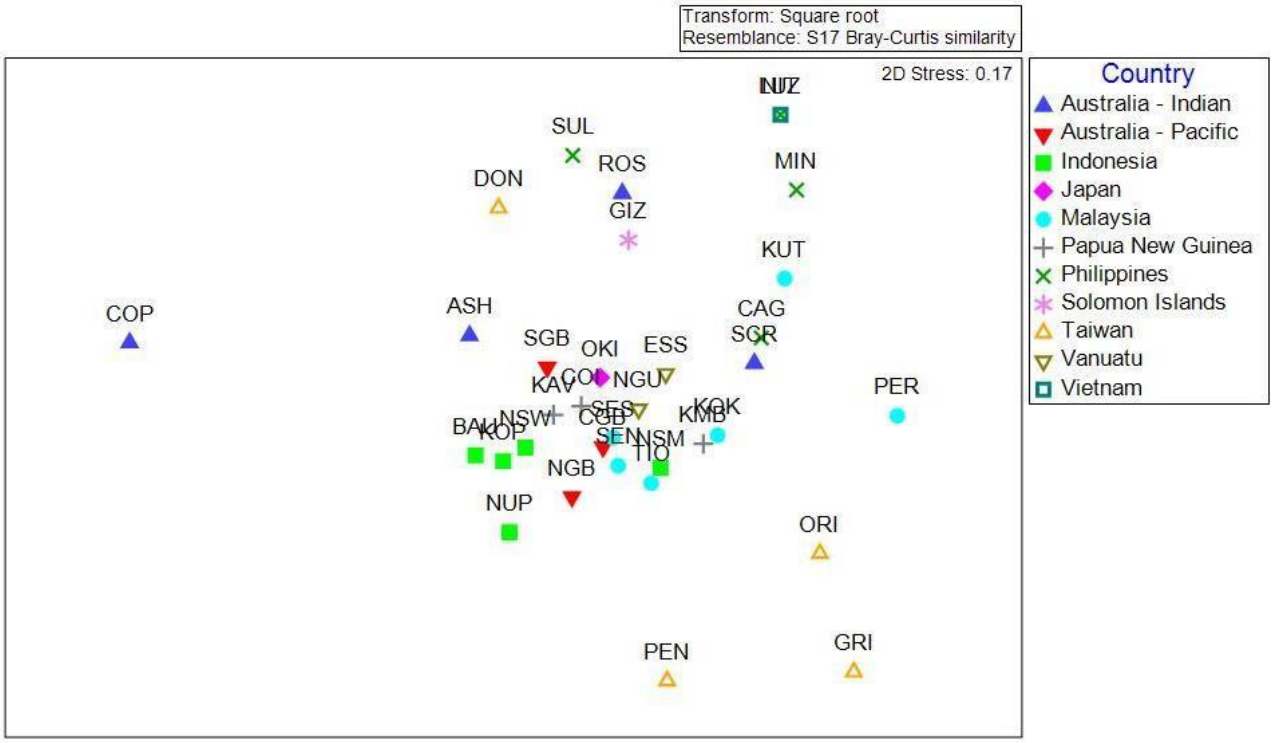


Figure 5.4. nMDS plot of all sites in which at least a single ray was observed. A 2-D stress of 0.17 was calculated. Three Taiwan sites separated from the grouping. Additionally, the three Great Barrier Reef sites were in close proximity to the Indonesian and Malaysian sites. Site codes found in ***Appendix I***.

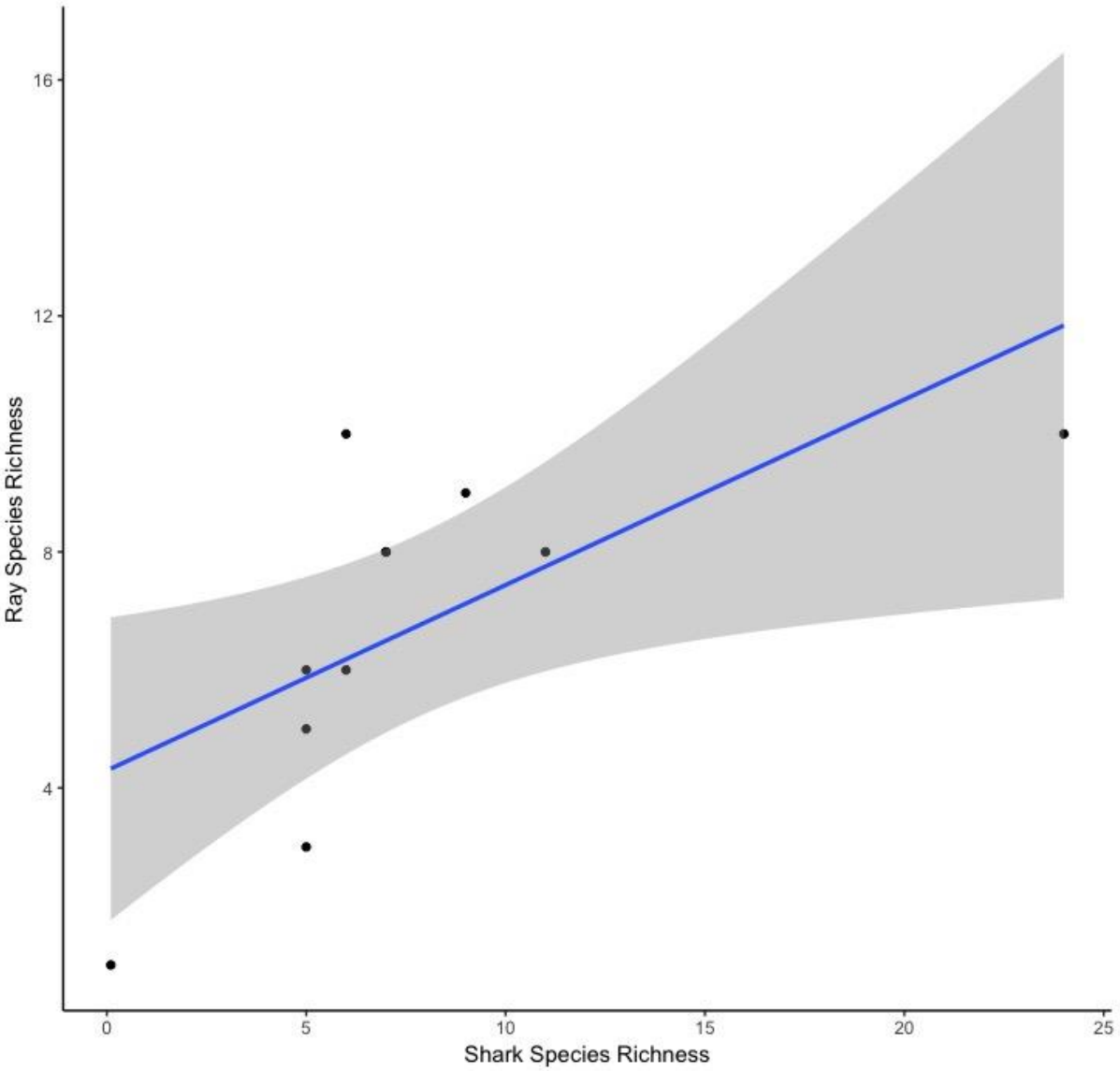


Figure 5.5. Ray species richness significantly increased with increasing shark species richness as shown by a simple linear regression.

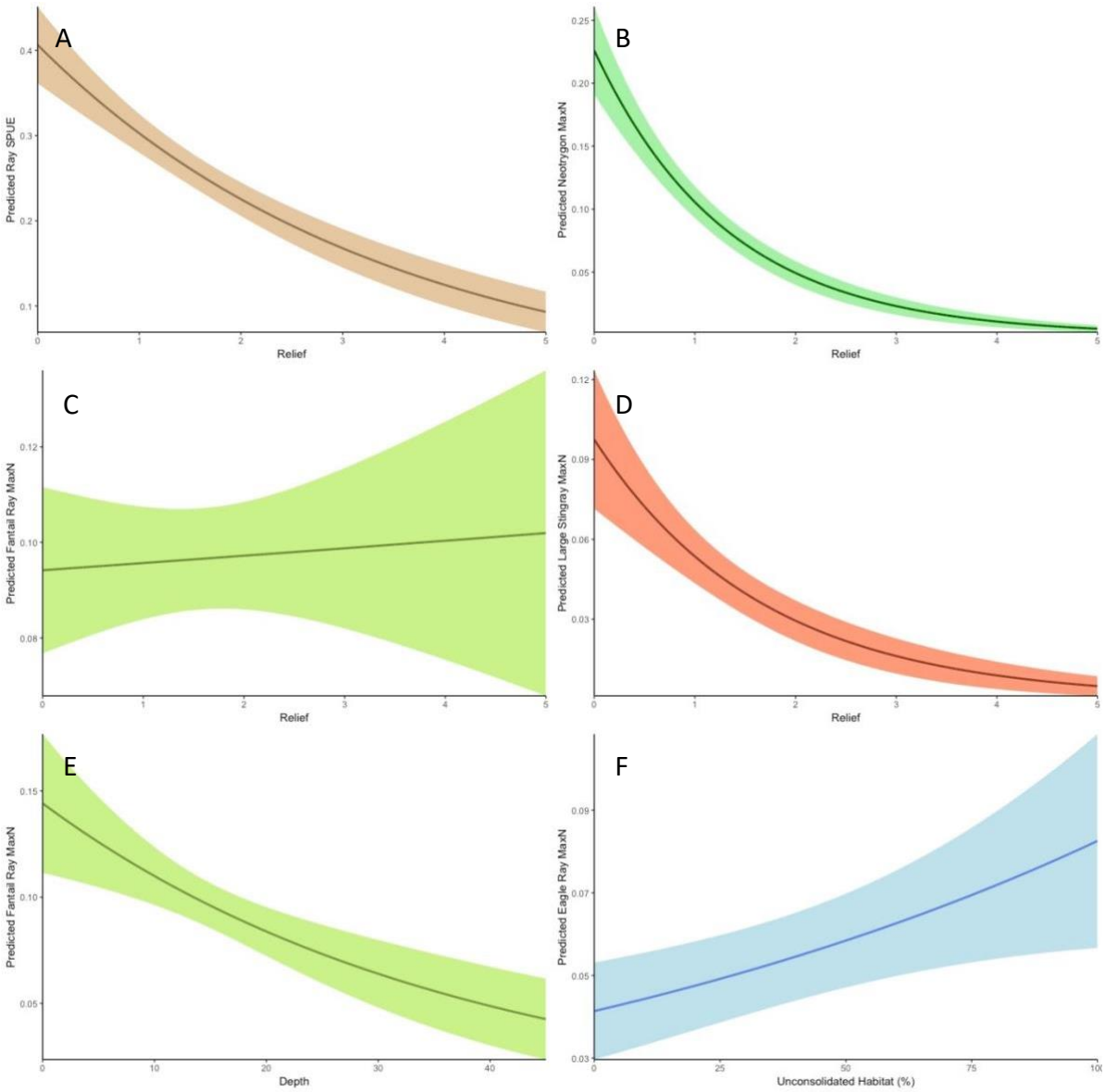


Figure 5.6. Effects of relief on predicted (A) SPUE of rays overall, (B) maskray MaxN, (C) fantail ray MaxN, and (D) large stingray MaxN as well as predicted effects of depth (E) for fantail ray MaxN and unconsolidated habitat (F) for eagle ray MaxN in 11 countries across the Coral Triangle and Australasian regions. Colours for maskrays, fantail rays, and eagle rays align with colours of species in figure 5.1. Lines indicate model predictions and shaded areas are 95% confidence intervals.

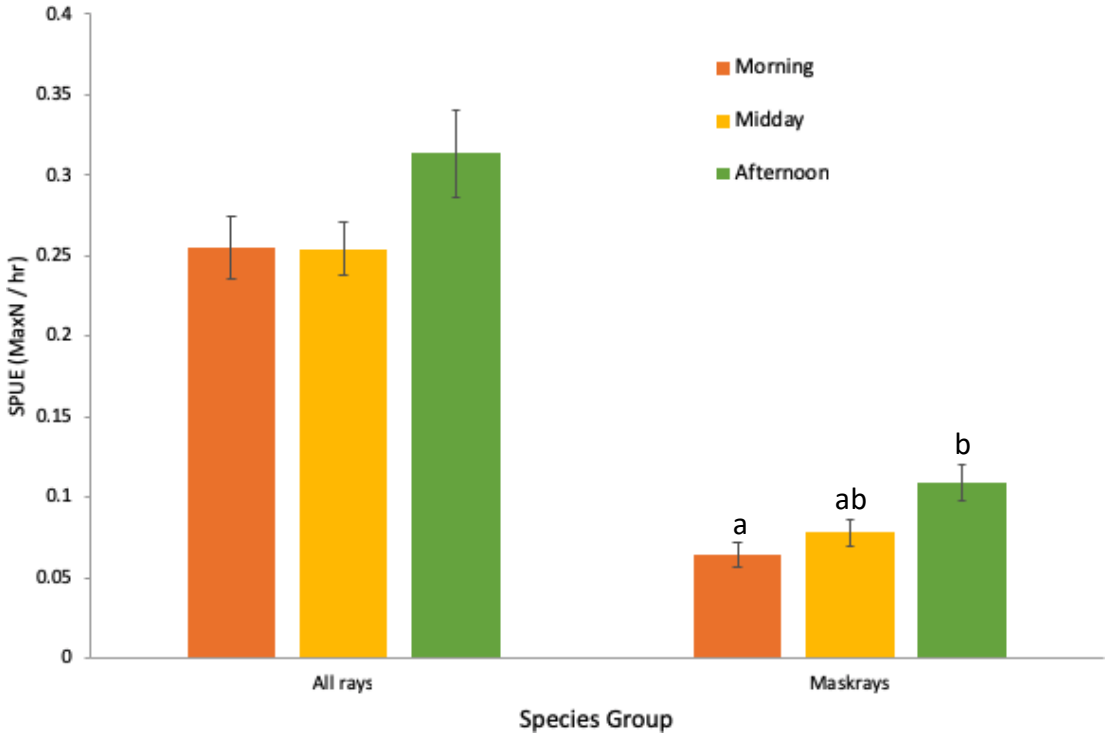


Figure 5.7. SPUE of rays overall and maskrays increased throughout the day. Only maskrays showed a significant increase in abundance from morning to afternoon. Homogeneous groups are indicated by letters. Rays overall increased from morning and midday to afternoon, however, this difference was not significant.

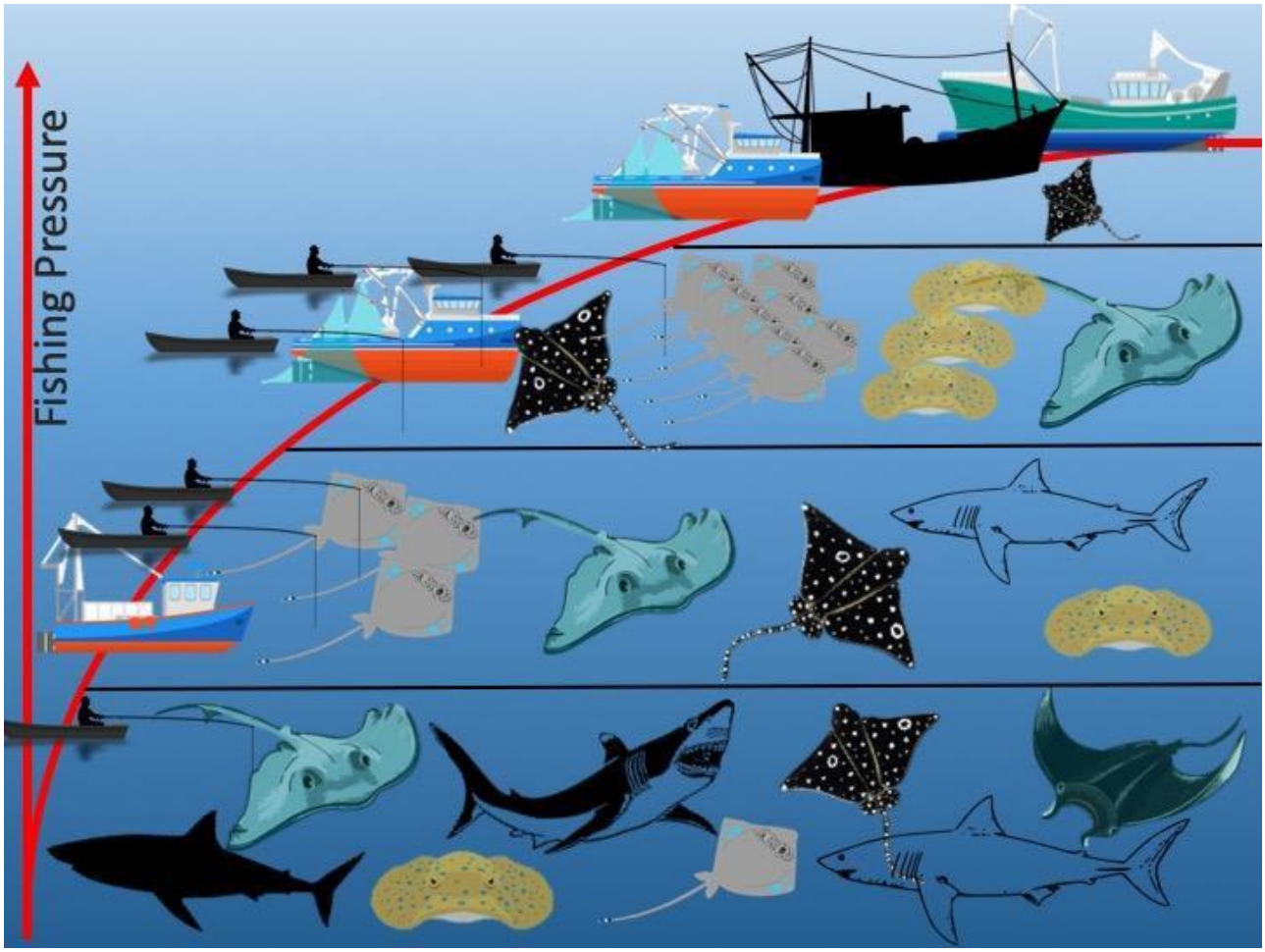


Figure 5.8. Elasmobranch assemblage changes with increasing fishing pressure based on results from this study. Initially, with limited fishing pressure there is a shark dominated system with high ray richness but low to moderate abundances. As fishing pressure increases, sharks are fished out leading to increased ray abundance and a speciose ray dominated community. A further fishing pressure increase leads to an ecosystem where sharks are functionally extinct leaving a completely ray dominated system with high abundances due to decreased predation risk and high abundances of small, productive ray species. Finally, when fishing pressure is too high for productive species to sustain their populations, the elasmobranch community is almost entirely removed with few, likely transient species present.

Table 5.1. Relative fishing pressure (based on catch reports from FAO, 2019), management and enforcement levels for fisheries in each country included in this study based on external sources ranked at low, medium, or high. Ray diversity refers to the number of species observed. Ray abundance is the ranking of the sightings per unit effort (SPUE) of rays at each country with 1 being the highest abundance and 11 being lowest.

Country	Fishing Pressure	Management	Compliance and Enforcement	References for Management and Compliance	Ray Diversity (# species)	Ray Abundance (Ranking)
Australia (Indian)	Medium	High	High	Prescott and Bentley (2009) Simpfendorfer et al. (2019)	8	2
Australia (Pacific)	Medium	High	High	Prescott and Steenbergen (2017) Simpfendorfer et al. (2019)	10	5
Indonesia	High	Low	Low	Yuliana et al. (2016) Prescott and Steenbergen (2017) Lieng et al. (2018) Muawanah et al. (2018) Pers. obs (2016-2019)	10	1
Japan	High	High	Medium	Pomeroy and Berkes (1997) Tokunaga et al. (2019)	5	6
Malaysia	High	Medium	Low	Lack and Sant (2009) Arai (2015) Pers. obs (2013-2017)	8	3
Papua New Guinea	Medium	Medium	Low	Cinner et al. (2005) Brown (2015) Siar et al. (2015) Leontine Baje (pers. comms)	9	4
Philippines	High	Medium	Medium	Pomeroy and Berkes (1997) Green et al. (2003) Samoilys et al. (2007)	6	10

				Yang and Pomeroy (2017)		
Solomon Islands	Low	Low	Medium	Hylton et al. (2017) Schwarz et al. (2017)	3	8
Taiwan	Medium	Medium	Medium	Shu (2014) Liao et al. (2019) Paul Clerkin (pers. comms)	8	9
Vanuatu	Low	Low	Medium	Hickey and Johannes (2002) Léopold et al. (2013)	6	7
Vietnam	High	Low	Low	van Zwieten et al. (2002) Ho et al. (2016)	1	11

Table 5.2. List of potential species that comprise the four groups of rays with indistinguishable species: eagle rays, maskrays, manta/devil rays, and wedgefish.

Species Group	Common Name	Latin Name	Species Authority
Eagle rays	*Aetomylaeus maculatus*	Mottled eagle ray	Gray, 1834
	Aetomylaeus caeruleofasciatus	Bluebanded eagle ray	White, Last and Baje, 2015
	Aetomylaeus nichofii	Banded eagle ray	Bloch and Schneider, 1801
	Aetomylaeus vespertilio	Ornate eagle ray	Bleeker, 1852
	Myliobatus hamlyni	Purple eagle ray	Ogilby, 1911
	Aetobatus ocellatus	Spotted eagle ray	Kuhl, 1823
Maskrays	*Neotrygon annotata*	Plain maskray	Last, 1987
	Neotrygon australiae	Australian bluespotted maskray	Last, White and Séret, 2016
	Neotrygon caeruleopunctata	Bluespotted maskray	Last, White and Séret, 2016
	Neotrygon kuhlii	Kuhl's maskray	Müller and Henle, 1841
	Neotrygon leylandi	Painted maskray	Last, 1987
	Neotrygon ningalooensis	Ningaloo maskray	Last, White and Puckridge, 2010
	Neotrygon orientalis	Oriental bluespotted maskray	Last, White and Séret, 2016
	Neotrygon picta	Speckled maskray	Last and White, 2008
	Neotrygon trigonoides	Coral sea maskray	Castelnau, 1873
Manta / devil rays	*Mobula alfredi*	Reef manta ray	Krefft, 1868
	Mobula birostris	Giant manta ray	Walbaum, 1792
	Mobula kuhlii	Kuhl's devilray	Müller and Henle, 1841
	Mobula mobular	Giant devilray	Bonnaterre, 1788
	Mobula tarapacana	Chilean devilray	Philippi, 1892
	Mobula thurstoni	Bentfin devilray	Lloyd, 1908
Wedgefish	*Rhinchobatus australiae*	Bottlenose wedgefish	Whitley, 1939
	Rhinchobatus palpebratus	Eyebrow wedgefish	Compagno and Last, 2008

Table 5.3. Species information for all species included in this study. N videos refers to the number of videos the species appears in. Sum of MaxN refers to the total number of individuals observed across all countries. Eagle rays, maskrays, manta/ devil rays, and wedgefish could not be identified to species, therefore, all sighting were combined to a single grouping.

Family	Genus	Species	Common name	Species Authority	N videos	Sum of MaxN
Myliobatidae /Aetobatidae	*Aetomylaeus / Aetobatus / Myliobatus*	----------	Eagle Rays		137	194
Dasyatidae	*Himatura*	*australis*	Australian whipray	Last, White and Naylor, 2016	1	1
Dasyatidae	*Himatura*	*uarnak*	Coach whipray	Gmelin, 1789	10	10
Dasyatidae	*Himatura*	*leoparda*	Leopard whipray	Manjaji-Matsumoto and Last, 2008	?	?
Dasyatidae	*Neotrygon*	----------	Maskrays		286	330
Dasyatidae	*Pastinachus*	*ater*	Broad cowtail ray	Macleay, 1883	13	13
Dasyatidae	*Pateobatis*	*fai*	Pink whipray	Jordan and Seale, 1906	40	65
Dasyatidae	*Pateobatis*	*jenkinsii*	Jenkins' whipray	Annandale, 1909	5	5
Dasyatidae	*Taeniura*	*lessoni*	Oceania fantail ray	Last, White and Naylor, 2016	1	1
Dasyatidae	*Taeniura*	*lymma*	Bluespotted fantail ray	Forsskål, 1775	309	328
Dasyatidae	*Taeniurops*	*meyeni*	Blotched stingray	Müller and Henle, 1841	26	28
Dasyatidae	*Urogymnus*	*asperrimus*	Porcupine whipray	Bloch and Schneider, 1801	1	1
Dasyatidae	*Urogymnus*	*granulatus*	Mangrove whipray	Macleay, 1883	21	22
Mobulidae	*Mobula*	----------	Manta / devil rays		16	28
Rhinidae	*Rhynchobatus*	----------	Wedgefish		25	25
Rhinobatidae	*Rhinobatos*	*hynnicephalus*	Ringed guitarfish	Richardson, 1846	1	1

Table 5.4. P-values of the Tukey HSD Post-hoc test of SPUE (rays/hour) between countries. Bolded numbers indicate country pairings with significantly different SPUEs. AUI – Australia - Indian Ocean, AUP – Australia - Pacific Ocean, IDN – Indonesia, JPN – Japan, MYS – Malaysia, PNG – Papua New Guinea, PHL – Philippines, SLB – Solomon Islands, TWN – Taiwan, VUT – Vanuatu, and VNM – Vietnam.

	AUI	AUP	IDN	JPN	MYS	PNG	PHL	SLB	TWN	VUT	VNM
AUI	---										
AUP	0.642	---									
IDN	**0.000**	**0.000**	---								
JPN	0.952	1.000	**0.000**	---							
MYS	1.000	0.897	**0.000**	0.994	---						
PNG	1.000	0.980	**0.000**	0.998	1.000	---					
PHL	**0.000**	**0.046**	**0.000**	0.583	**0.000**	**0.002**	---				
SLB	0.422	0.994	**0.000**	1.000	0.644	0.778	0.984	---			
TWN	**0.004**	0.466	**0.000**	0.941	**0.011**	0.057	0.998	1.000	---		
VUT	0.256	0.966	**0.000**	1.000	0.477	0.698	0.770	1.000	0.996	---	
VNM	**0.000**	**0.036**	**0.000**	0.361	**0.000**	**0.002**	1.000	0.886	0.945	0.520	---

Table 5.5. Top GLMM models for predicting SPUE (rays/hour), and genera specific models for the four most abundant species / species groups. Difference between lowest corrected Akaike Information Criterion (ΔAICc), AIC weights (wAICc), and biggest VIF value of all variables in the model (Biggest VIF) are reported. Model selection was based on the most parsimonious model within two units of the lowest ΔAICc and with the biggest VIF value <5. Selected models are presented in bold. Variable codes: Relief - on a scale of 0-5 with increasing complexity, Time.of.Day – time of BRUVS deployment (morning, midday, afternoon), H.Unconsol – percent unconsolidated habitat, logGravityCities – weight of human activities based on human population and access to environment.

Species / Species Group	Best Model	ΔAICc	wAICc	Biggest VIF
SPUE (rays / hour)	**Country + Relief + Time.of.Day**	**0**	**0.38**	**1.04**
	Country + Relief + Depth	0.57	0.29	1.06
	Country + Relief	1.43	0.19	1.03
	Null	85.67	0	-
Maskrays	**Country + Relief + Time.of.Day**	**0**	**0.74**	**1.04**
	Country + Relief	2.87	0.18	1.03
	Country + Relief + Depth	4.89	0.06	1.06
	Null	160.43	0	-
Fantail rays	**Country + Relief + Depth**	**0**	**0.80**	**1.06**
	Country + Depth	2.79	0.20	1.03
	Country + H.Unconsol	14.48	0	1.03
	Null	48.86	0	-
Eagle rays	**H.Unconsol**	**0**	**0.51**	**-**
	logGravityCities + Relief	2.30	0.16	1.00
	Country * Relief	3.18	0.10	2.83
	Null	16.28	0	-
Large stingrays	Relief * Depth	0	0.21	5.17
	Country + Relief + Time.of.Day	0.83	0.15	1.04
	Country + Relief	**1.31**	**0.11**	**1.03**
	Null	34.78	0	-

Chapter 6

When Sharks are Away Rays Will Play: Effects of Top Predator Removal in Coral Reef Ecosystems

Plate 6. The most common ray and shark species on BRUVS throughout Southeast Asia and the Western Pacific (top = nine maskrays in Bau Bau, Indonesia; bottom = four grey reef sharks in the Great Barrier Reef, Australia).

6.1 Introduction

Rays play important roles in coral reef ecosystems, providing energetic links between trophic levels and habitats and oxygenating sediments through bioturbation (Martins et al. 2018). However, their interactions with higher trophic levels within their ecosystems are poorly known. Sharks act as predators on rays, and therefore have the potential to affect their abundance and behaviour (Heithaus et al. 2008; Ferretti et al. 2010). Prey abundances are directly affected by predation, while prey behaviours are also affected indirectly due to predation risk. Sharks have been suggested to play a vital role in coral reef ecosystem health through direct predator-prey interactions, and also affecting genetics, movement and condition of their prey species (Ruppert et al. 2016). This role, however, is debated, with Roff et al. (2016) speculating sharks have less influence on coral reef ecosystems than purported. If sharks do have an impact on coral reef condition, their decline should be followed by measurable ecosystem changes.

In areas where shark abundances are significantly reduced, mesopredator release, where the abundance of mesopredators increases substantially following predator declines, has been reported (Ward and Myers 2005; Valinassab et al. 2006). The predator-prey relationship has been extensively studied across many marine taxa and through a variety of sensory and behavioural influences including olfactory, visual, and auditory cues (Kelley and Magurran 2003; Slabbekoorn et al. 2010), flight initiation distances (McLean and Godin 1989), and foraging behaviour (Lima 1998). An important factor when considering this relationship is adaptive behaviour of both predator and prey (Anholt and Werner 1998; Lima 2002; Abrams and Matsuda 2005). In the absence of predators, prey species are able to forage more boldly and dedicate more time and resources to reproduction (Peacor 2002). When predators are abundant, prey behaviour is directly linked to their survivorship, such

that risk taking individuals have lower survival than non-risk takers (Kelley and Magurran 2003; Heithaus et al. 2012). Predation risk, therefore, may influence prey movement patterns and behaviours, making the interpretation of prey abundance more complex.

Shark predation on rays has been well documented through diet and observational studies (Strong Jr. et al. 1990; Lucifora et al. 2009; Marshall and Bennett 2010). Rays are a preferred prey of species such as hammerhead sharks (*Sphyrna* spp.)(Strong Jr. et al. 1990) and many reef sharks also have documented diets that include rays (Papastamatiou et al. 2006). For example, blacktip reef sharks (*Carcharhinus melanopterus*) have been found with ray remains in their stomachs (Lyle 1987) and lemon sharks (*Negaprion acutidens*) have been observed with stingray barbs in their mouths (J. Mourier, pers. comm). Recently, it was noted that shark-like batoids (Families: Glaucostegidae, Rhinobatidae, and Rhinidae) also consume their stingray relatives, confirmed in several species that presented with stingray spines embedded in their jaws (Dean et al. 2017). In some cases, predation events are nonlethal (Fitzpatrick et al. 2006; Marshall and Bennett 2010), but can have harmful effects on the individual's fitness (Harris 1989). Therefore, it would be beneficial for rays to avoid areas with high predator abundance or employ behavioural mechanisms that reduce their predation risk and hence increase fitness.

Rays have developed several strategies to reduce their risk of predation. Some use aggregating or grouping behaviours including "piggybacking" (Meekan et al. 2016) and resting in mixed species groups for rapid warning of predatory threats (Semeniuk and Dill 2005). Mixed groups provide added safety as some species respond faster to certain hazards than others (Semeniuk and Dill 2005; Semeniuk and Dill 2006). Selective habitat use is another predator avoidance strategy that appears to be used by a large variety of

rays (Vaudo and Heithaus 2009; Whitty et al. 2009; Bond 2015). By using habitats where predator abundances are low, rays can reduce their predation risk.

Given the predator-prey relationship between sharks and rays, it would be predicted that locations with reduced levels of shark abundance would have higher abundances of rays in the absence of other threats. While such a hypothesis has rarely been tested, there is evidence to support it. For example, in the Persian Gulf and Oman Sea, trawl surveys performed up to 28 years apart showed a significant decline in shark abundance and a significant increase in ray abundance (Valinassab et al. 2006). It is unclear, however, whether the increase in ray abundance was directly due to the decrease in shark abundance. Some studies have speculated that ray populations are more likely to be reduced with increasing shark predation than teleosts and cephalopods due to their life history characteristics of low fecundity and slow growth (Heithaus et al. 2008). Although a causative link has not been identified, several studies have shown increases in mesopredator elasmobranch abundances following decreases in top predator abundance (Shepherd and Myers 2005; Ferretti et al. 2010).

The aims of this paper were to: (1) examine differences in abundances of two genera of small benthic rays between sites with varying shark and shark-like batoid abundances (hereafter collectively called 'predators'), and (2) explore behavioural differences between rays at sites with varying predator abundances. We hypothesized that the focal species would be more abundant at sites with lower predator abundance due to mesopredator release. In addition, we also predicted the focal species would exhibit bolder behaviour at sites with lower predator abundance due to decreased risk and that these behavioural differences may confound the estimation of abundance.

6.2 Methods

6.2.1 Study Sites

Nineteen reefs spread amongst 12 sites across six countries in Southeast Asia and the Western Pacific were sampled with Baited Remote Underwater Video Systems (BRUVS) between December 2015 and June 2018 (**Figure 6.1**; ***Appendix III***). Sites were selected across a range of shark fishing intensities (see: **Table 5.1**) to provide contrast in predator abundances.

6.2.2 Sampling

BRUVS were deployed at nineteen reefs with up to six units deployed simultaneously during daylight hours. BRUVS were deployed a minimum of 500 m apart at 1.5 m to 48.6 m depth in coral reef and reef associated habitats for a minimum of one hour. Deployments spanned a variety of habitat types including reef crest, slope, and adjacent seagrass, lagoon, and sand flats. Single and stereo BRUVS were used in this study. Single BRUVS units consisted of aluminum frames that housed a GoPro Hero 4 Silver camera with wide angle view (approx. 170° in air), (1920 X 1080 video format, 30 frames/s) housed in NiMAR housings. Stereo BRUVS consisted of an aluminum frame with two GoPro Hero 4 Silver cameras in custom housings with medium angle view (approx. 120° in air), (1920 x 1080 video format, 30 frames/s). In both BRUVS units a bait arm extended 1-2 m from the frame containing 1 kg of the oiliest fish available in each location. In decreasing order, bait used was: pilchards (*Sardinella* spp.), slimy mackerel (*Scomber australasicus*), tuna (*Thunnus* spp.), fusilier (*Caesio* spp.), wahoo (*Acanthocybium solandri*), and coral trout (*Plectropomus leopardus*).

6.2.3 Species

This study focused on two genera of small rays, the genus *Neotrygon* (bluespotted maskrays), and genus *Taeniura* (fantail rays). These genera were selected as they occur widely across the sampling area and are comprised of smaller species that are likely to be prey of a suite of predators, including elasmobranchs and large teleosts, throughout their lives (Dabruzzi et al. 2013).

The *Neotrygon* complex consists of up to six species (*N. annotata* Last 1987, *N. australiae* Last, White & Séret 2016, *N. caeruleopunctata* Last, White & Séret 2016, *N. kuhlii* Müller & Henle 1841, *N. orientalis* Last, White & Séret 2016, and *N. trigonoides* Castelnau 1873) found within the range of this study, but indistinguishable on BRUVS footage due to morphological similarities. The largest *Neotrygon* species can attain a disc width (DW) of up to 47 cm (Last et al. 2016). Size at maturity varies by region and species and can range from 24.5 – 30.5 cm DW for males in Indonesian waters (Fahmi et al. 2009). *Neotrygon* species are abundant throughout Southeast Asia but are heavily fished both directly and as bycatch and used for their meat (Fahmi et al. 2009; Last et al. 2010). Their abundances in the Western Pacific are poorly known.

There are two species in the genus *Taeniura*: the bluespotted fantail ray (*Taeniura lymma* Forsskål, 1775) and the Oceania fantail ray (*Taeniura lessoni* Last, White & Naylor 2016). *Taeniura lymma* attains a DW of at least 35 cm (Last et al. 2010). Size at maturity ranges from 20 – 24 cm DW for both species. *Taeniura lessoni* attain a DW of at least 22 cm and are found in the Solomon Islands (Last et al. 2016). Both *Taeniura* species are abundant in coral reef habitats across their range and are fished in smaller quantities than *Neotrygon* species. (Last et al. 2010).

6.2.4 Video annotation

All BRUVS footage was analysed by two independent annotators using either Event Measure (www.seagis.com v.4.43) or FinPrint Annotator (v.1.1.44.0). Annotators marked the arrival time of every individual elasmobranch that entered the screen throughout the video. The maximum number of individuals of the same species in a single frame was marked (MaxN) for each elasmobranch species. A senior reviewer validated species identification and compared the two reads of each video. All videos containing the focal species were then reanalysed by a senior reviewer. Where possible individual rays were identified by their unique markings to obtain MaxIND (Sherman et al. 2018) and timed from the first frame they entered in view to the last frame before they exited the screen. Rays were identified as either 'transient' or 'resident', the former descriptor being attributed to individuals that entered and exited in a straight line far from the BRUVS and did not re-visit throughout the deployment, while residents appeared in frame close to the BRUVS unit and did not travel in a straight line while in view. Any feeding activity on the bait bag by the focal species was documented.

6.2.5 Relative Abundances

Shark abundances at each reef were estimated using the sum of the MaxN of all potential predators of small benthic rays (***Appendix IV***) within the elasmobranch subclass from each deployment. This sum was then converted using sightings per unit effort (SPUE) for each deployment by dividing by the deployment time in hours. The mean predator SPUE was then calculated for each reef. Predator SPUE for each reef was then used as a dependent variable in the models.

Ray abundances were similarly estimated. Rather than using MaxN, the total number of

individuals (MaxIND) was used. This was then converted using sightings (individuals) per unit effort (SPUE) for each deployment by dividing by deployment time in hours.

6.2.6 Environmental Drivers

Date, time, depth (m), and wind speed (Beaufort scale) were recorded at the time of each BRUVS deployment. Time of day was split into three categories: morning (deployment before 10:29), midday (deployment from 10:30-13:29), and afternoon (deployment after 13:30). Using BenthoBox software (www.benthobox.com) visibility, relief, and habitat were analysed for each deployment. Visibility was categorized in 2 m bins (0-2, 2-4, 4-6, 6-8, 8-10, and 10+ m). Relief and habitat were analysed by placing a 20 square grid over an image from the deployment. All squares containing any benthos were given a relief score from 0 (flat) to 5 (complex) and the average relief was calculated. Habitat was similarly analysed with a 20 square grid over an image from the deployment. The main habitat type within each square was identified and assigned a benthic category, and percent cover of the entire site was calculated based on the total number of squares containing benthos and the total number of squares with each benthic category. Categories included hard coral, soft coral, bleached coral, unconsolidated (sand/rubble), consolidated (rock), seagrass, turf algae, macroalgae, and other (cnidarians, sponges, etc.). Habitat categories that appeared on less than 5% of deployments were excluded from further analyses (bleached coral – 0.48% of deployments, seagrass – 1.03%, and other – 2.86%).

6.2.7 Data Analyses

R (version 3.5.1) was used for all statistical analyses. Pearson correlation analyses were performed on all numeric variables to determine any correlated factors. Wind and visibility were each highly correlated with both site and reef and were both removed from further

analyses. The association with predator abundance on ray abundance and time spent in frame for each 'resident' individual, were estimated using generalized linear mixed models (GLMM) using template model builder (R package - glmmTMB (Brooks et al. 2017)). To accommodate the large number of zeros in the abundance data, zero-inflated and negative binomial GLMM models were tested. Negative binomial models outperformed zero-inflated models and were used for final analyses. A zero-inflation value of 1 was included in all models and country, site, and reef were included as random variables. The effect of predator abundance on the number of visits by individual rays was analysed using a hurdle model with a negative binomial distribution (R package – pscl (Jackman et al. 2017)). A hurdle model was used because positive count data eliminates videos with no rays, thus removing the bias these BRUVS would include. A negative binomial generalized linear model was run with positive- count data based on results from the hurdle model (R package – MASS (Ripley et al. 2018)).

Model selection for GLMMs was performed using an Akaike Information Criteria (AIC) test on 15 proposed models and a null model (Akaike 1998) including all environmental variables and predator abundance. The most parsimonious model (least number of variables) with an AIC value within two units of the lowest AIC value was selected as the best performing model (Burnham and Anderson 2004). All model variables were tested for collinearity using variance inflation factors (VIF) and only those models with variables all consisting of values <5 were considered (Akinwande et al. 2015). Generalized boosted regression models (GBM) were run to determine the contribution of each factor included in selected models (R package – gbm (Greenwell et al. 2018)). GBMs were developed using all deployments with a tree complexity of 5, computer learning rate of 0.001, and a bag fraction of 0.5.

To analyse feeding behaviour, the total number of individuals that fed from the bait bag was calculated at the reef level for reefs where more than one individual was present. The percentage of 'resident' rays that fed at each reef was transformed with a log (X+1) function to normalize the distribution and linearly regressed against predator abundance. Due to the small sample size, both ray genera were combined for this analysis.

6.3 Results

6.3.1 Deployments

A total of 565 individuals of the focal species (309 *Neotrygon* spp. and 256 *Taeniura* spp.) were observed from 1257 BRUVS. A total of 678 predators were observed comprising 19 species. The most commonly observed predators were grey reef (*Carcharhinus amblyrhynchos*), blacktip reef (*Carcharhinus melanopterus*), and whitetip reef (*Triaenodon obesus*), respectively. These three species made up 85% of the predators observed in this study. Predator abundance was lowest in Malaysia – Mabul/Kapalai (SSMK), where no predators were observed. Highest abundance was observed in the Solomon Islands East (SIEA) with a SPUE of 1.68 ± 0.23 predators hr^{-1} (**Fig. 6.2**).

6.3.2 Relative Abundance

Ray SPUE was highest at Malaysian reefs SSMK and SNTS with abundances of 1.15 ± 0.32 individuals hr^{-1} (ind hr^{-1}) and 0.64 ± 0.11 ind hr^{-1}, respectively, and at Indonesian reefs IDKE and IDKW with SPUEs of 0.73 ± 0.12 ind hr^{-1} and 0.69 ± 0.10 ind hr^{-1}, respectively (**Fig. 6.2**). The focal species were completely absent from four reefs: AMSS in American Samoa, SSS in Malaysia, SIEA in Solomon Islands and ESVT in Vanuatu (**Fig. 6.2**). Rays were present on 241 of 1257 (19.2%) BRUVS deployments. Of these, *Neotrygon* spp. were present on 113 BRUVS (SPUE = 2.75 ± 0.48 ind hr^{-1} when present) and *Taeniura* spp. were present on 144 BRUVS (SPUE = 1.78 ± 0.12 ind hr^{-1} when present).

Ray abundance decreased as predator abundance increased, with GLMMs revealing a significant negative relationship between ray abundance (both genera) and predator abundance (z-value = -2.976, p = 0.003)(**Table 6.1**). This relationship had a significantly steeper slope for *Taeniura* spp. than *Neotrygon* spp. (z-value = 3.171, p = 0.002)(**Fig. 6.3a**). There was a significant effect of depth on small ray abundance such that deeper deployments had lower small ray abundances (z-value= -5.187, p<0.001). This relationship was significantly different between the two genera; *Neotrygon* spp. occurred at significantly greater depths than *Taeniura* spp. (z-value=3.780, p<0.001)(**Fig. 6.3b**). There were also significant differences in abundance at varying levels of relief for *Neotrygon* spp. which were found in lower relief habitats than *Taeniura* spp. (z-value= -6.713, p<0.001)(**Fig. 6.3c**). A GBM indicated depth, relief, and predator abundance all had relative influences of between 24% and 30% on small ray abundances, whereas genus contributed 18.3% (**Fig. 6.4**).

6.3.3 Ray Behaviour

There were a total of 957 visits to BRUVS by small ray species across 1257 deployments. Of those visits, 465 were by *Neotrygon* spp. (1.51 ± 0.07 visits per individual) and 492 were by *Taeniura* spp. (1.92 ± 0.16 visits per individual). The zero-count hurdle model for visits identified similar factors affecting ray abundance as the GLMM models identified for abundance (**Table 6.1**). Relief had the greatest relative influence on ray visits (31.0%), followed by depth (28.0%), predator abundance (24.2%) and finally, genus (16.8%)(**Fig. 6.4**).

For the positive-count hurdle model, a significant negative relationship was found between the number of visits and predator abundance (z-value= -2.234, p= 0.026). There was no significant difference between genera (z-value= 0.023, p= 0.981). Neither relief nor depth significantly affected the number of visits by an individual (z-value = 0.916, p = 0.360; z-

value = -0.425, p = 0.671, respectively). No significant differences were found between genera for number of visits with relief or depth (z-value = -1.139, p = 0.255; z-value = 0.286, p = 0.775, respectively). The negative binomial GLM revealed a significant negative relationship between the number of visits and predator abundance (z-value = -4.373, p<0.001)(**Fig. 6.5**). No significant difference was found between genera (z-value = 1.108, p = 0.268).

Over half of individuals were considered 'resident,' meaning they did not travel in a straight line in and out of frame (*Neotrygon* spp. 56.5%, *Taeniura* spp. 62.5%), but instead altered their path to swim around or interact with the bait bag. The largest proportion of a video (~60 minutes) an individual spent in frame was 59.9% for *Neotrygon* spp. and 62.5% for *Taeniura* spp.. There was a significant decrease in time spent in frame as predator abundance increased (GLMM, z-value = -2.340, p = 0.019). Focal species also spent significantly more time in frame at shallower depths (z-value = -3.276, p = 0.001), and in lower relief habitats (z-value = -6.155, p < 0.001). Depth had the greatest relative influence on proportion of time spent in frame (39.7%), followed by predator abundance and relief (30.8% and 29.5%, respectively)(**Fig. 6.4**).

Of the 335 'resident' individuals, 97 fed from the bait bag (29.0%). The proportion of individuals that fed from the bait bag at each site was significantly higher at sites with lower predator abundance as shown through a linear regression with a log (X+1) percent of small rays fed (t = -2.465, df = 1 and 12, p = 0.029).

6.4 Discussion

This study has revealed small ray abundance and behaviour are affected on coral reefs with high predator abundance, and that the level of decrease in abundance of *Taeniura* spp. was greater at any given level of predator abundance than for *Neotrygon* spp.. These findings provide evidence that shark loss on coral reefs may lead to increases in ray abundance, therefore providing evidence of mesopredator release. Additionally, these findings show that potential predator effects need to be specifically considered when interpreting abundances of prey species through surveys. Potential evidence for mesopredator release involving elasmobranchs was observed in the Persian Gulf and Oman Sea where trawl surveys performed caught high abundances of sharks initially, however, when resurveyed 30 years later high abundances of rays were caught with few sharks (Valinassab et al. 2006). While several studies have projected the connection between predator declines due to fishing and increases in mesopredator abundance (Valinassab et al. 2006; Heithaus et al. 2008; Ferretti et al. 2010), few have examined direct behavioural effects of predator abundance on mesopredators. In this study, we demonstrate that lower abundances of small rays were significantly correlated with higher predator abundances. Small rays also spent significantly less time in the field of view and did not make repeated visits to BRUVS when predator abundances were high. These are indicators of bolder behaviour by rays in lower predation risk areas. These results were similar to a BRUVS study in southern Australia where fish abundances and diversity were lower on videos in which sharks were present (Klages et al. 2014). Presence of predators has also been shown to reduce foraging in reef fish due to perceived predation risk (Rizzari et al. 2014). Therefore, predator presence likely affects the capacity to observe and accurately measure abundances of lower trophic level species. Few community composition studies consider the potential effects of animal behaviour and interactions on the interpretation of abundances despite their role in

driving which species are observed. The potential for predators to influence prey behaviour and abundance thus needs to be considered in ecosystem studies since behaviour plays an important role in animal movement and presence (Austin et al. 2004; Rasher et al. 2017). Community composition studies that use multiple sampling methods to reduce bias and increase species observed for analyses are likely to provide more accurate results (Boussarie et al. 2018). If a single sampling technique is used, such as BRUVS, it is important to understand the bias predator abundance may have on potential estimates of abundance data for lower trophic level species.

Marine reserve effectiveness is often measured by comparing shark abundances inside and outside of the reserves (Dulvy 2006; Bond et al. 2012; Espinoza et al. 2014). The presence of sharks, however, may make it difficult to estimate ray abundances. For example, a relatively common species could be interpreted as being rare due to the ability to observe them ("sightability") in high predator areas like marine reserves. A ray species may appear to have similar abundances within and outside of marine reserves but their sightability outside the reserve may be higher due to behavioural changes caused by lower predator abundances, as we observed in this study. Thus, behavioural changes may be artificially deflating their measured abundance masking the benefit of the marine reserve for those species. Furthermore, comparing diversity may not be accurate, as we have shown that individual species respond at different magnitudes of predator abundances. For example, in the Caribbean, large stingrays were found in lower abundances in marine reserves, where sharks were more abundant and those found within the reserve also had more visible bite marks (Bond 2015). Therefore, predator abundances may mask the true relative abundances of ray species and effectiveness of a marine reserve for mesopredator species.

The home ranges and movement potential of the focal species in this study are unknown. However, recaptures of several blue-spotted maskrays within the same bay after up to three years at liberty suggests high site fidelity (Pierce and Bennett 2009). Other studies on reef associated stingrays have shown their home ranges to be small, <0.5 km^2 in some species (Tilley et al. 2013b; Davy et al. 2015). Based on these studies, and the association of both focal ray genera with coral reef habitats, the individual rays in this study are likely to be resident to the reefs at which they were observed. This means results in this study are likely a response to differences in predator abundance and not immigration/emigration.

In areas with higher predator abundances, prey species must employ strategies to avoid predation. In an Australian mangrove-lined bay, juvenile rays avoided predators by remaining within mangroves habitats at high tide, and staying in shallow water throughout low tide periods to avoid predators (Davy et al. 2015). Both focal species genera in this study also appear to employ predator avoidance strategies including spending less time in open areas (in view of the camera) and visiting the BRUVS fewer times where predator abundances were higher. These strategies do reduce sightability of rays, however, due to the magnitude of difference we found in ray abundances at low and high predator abundances, our conclusions of mesopredator release are well-founded.

We showed that small reef associated rays were less likely to feed from the bait bag at sites with higher predator abundances. Feeding activity of mesopredator species has been shown to decrease when predation risk is high on coral reefs (Trussell et al. 2003; Rizzari et al. 2014; Lönnstedt et al. 2018; Madin et al. 2019). The focal species feed on benthic infauna that inhabit sandy patches within or adjacent to reefs (O'Shea et al. 2013; Pardo et al. 2015).

In order to access prey, they are required to forage in open sand areas where they may be at risk of predation, making food acquisition a risky endeavour (Anholt et al. 2000; Heithaus and Dill 2002). Additionally, in order to feed, rays disturb the benthos excavating sediment to find their prey (O'Shea et al. 2012b). This action may alert predators to their location, therefore, a reduction in foraging could reduce predation risk, particularly in areas with high predator abundances. Where predation risk is lower, increased foraging activity could allow rays to put more energy into growth and reproduction (Werner and Anholt 1993).

In addition to predator abundance and behavioural differences, we found small ray abundance differed significantly with environmental variables. *Taeniura* spp. preferred shallower, and higher relief areas than Neotrygon spp. This was expected as *Neotrygon* spp. are found in sandy habitats adjacent to coral reefs, while *Taeniura* spp. are more often found within the reef, hiding under rocks and corals (Last et al. 2016)(pers. obs). *Taeniura* spp. abundance decreased such that at any given predator abundance they were significantly more affected than *Neotrygon* spp. to increasing predator abundance. This result may be due to the higher potential of predator encounters in high relief areas. The most commonly observed sharks across all sites were reef sharks (*C. amblyrhynchos, C. melanopterus,* and *T. obesus*), which prefer high relief coral habitats (Wass 1971; Espinoza et al. 2014; Heupel et al. 2018). Therefore, high use areas for *Taeniura* spp. overlap with high use areas for reef sharks more than with *Neotrygon* spp. Additionally, availability of a refuge, like coral on a reef, has been shown to increase anti-predator responses in other marine species (Lehtiniemi 2005).

In Southeast Asia, rays are fished at the highest rate globally (Dulvy et al. 2017). While shark landings may be decreasing slightly (Davidson et al. 2016), ray landings in Indonesia

increased in the early 2000s and they are still caught and sold in markets across the country (White and Dharmadi 2007; Nijman and Nekaris 2014). Intense fishing pressure can have a large negative effect on elasmobranch abundances as seen in the Arabian Gulf (Jabado et al. 2018). In the present study, the opposite was observed for the two small-bodied genera of rays. Jabado et al. (2018) found a SPUE of 0.15 rays hr^{-1} in a heavily fished environment (SPUE of 0.06 predators hr^{-1}), whereas our study found a SPUE of >0.60 rays hr^{-1} in 4 out of 7 sites in Malaysia and Indonesia (SPUE of 0.0 to 0.17 predators hr^{-1}). This was compared to a SPUE of <0.15 rays hr^{-1} in 5 out of 7 sites in Australia and Vanuatu, which have relatively low fishing pressure and higher predator abundance (SPUE of 0.20 to 1.48 predators hr^{-1}). These results indicate that *Taeniura spp.* and *Neotrygon* spp. may be highly productive, particularly in low predator areas and thus able to support significant fishing pressure. Additionally, *Neotrygon* spp. in Indonesia exhibit plasticity in their life history characteristics between locations (Fahmi et al. 2009). This plasticity is possibly an adaptation to differing fishing pressures and environmental changes (i.e. smaller size at maturity increases lifetime fecundity). However, these characteristics may also be influenced by predator abundance such that in areas with higher predator abundances it is more beneficial to grow large first to reduce predation risk and then begin reproducing (Van Buskirk and Yurewicz 1998).

Data from 19 reefs in Southeast Asia and the Western Pacific indicated lower predator abundance was related to increases in small ray abundance on coral reefs suggesting the loss of higher predators likely has a cascading effect on coral reef ecosystems via mesopredator release. This effect potentially extends to lower trophic levels as well. In addition to abundance, behavioural differences occur in small rays between different levels of predator abundances that must be considered when investigating the ecological consequences of predator loss.

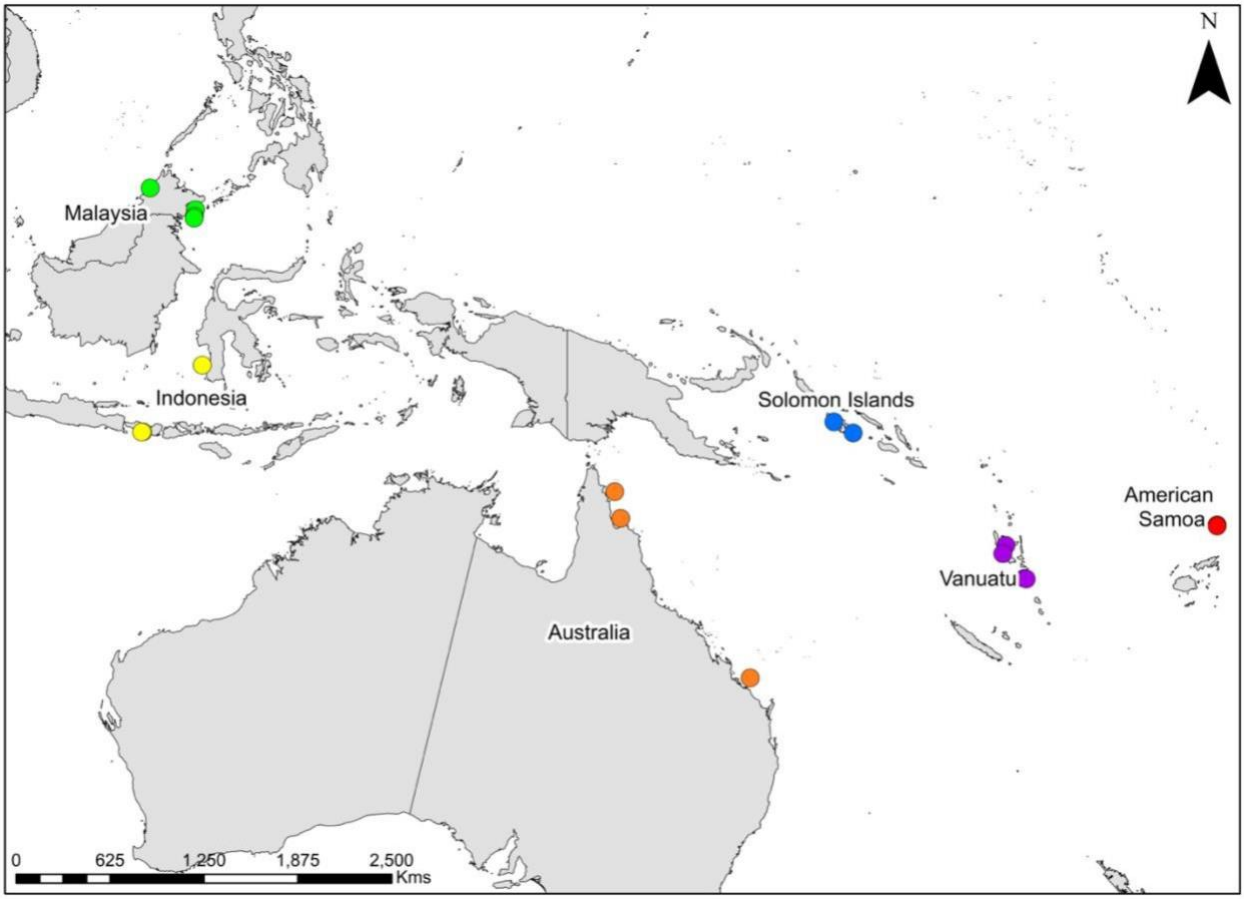


Figure 6.1. Map of sites surveyed. Each circle represents one site. Circle colour indicates country: American Samoa – red, Australia – orange, Indonesia – yellow, Malaysia – green, Solomon Islands – blue, Vanuatu – purple.

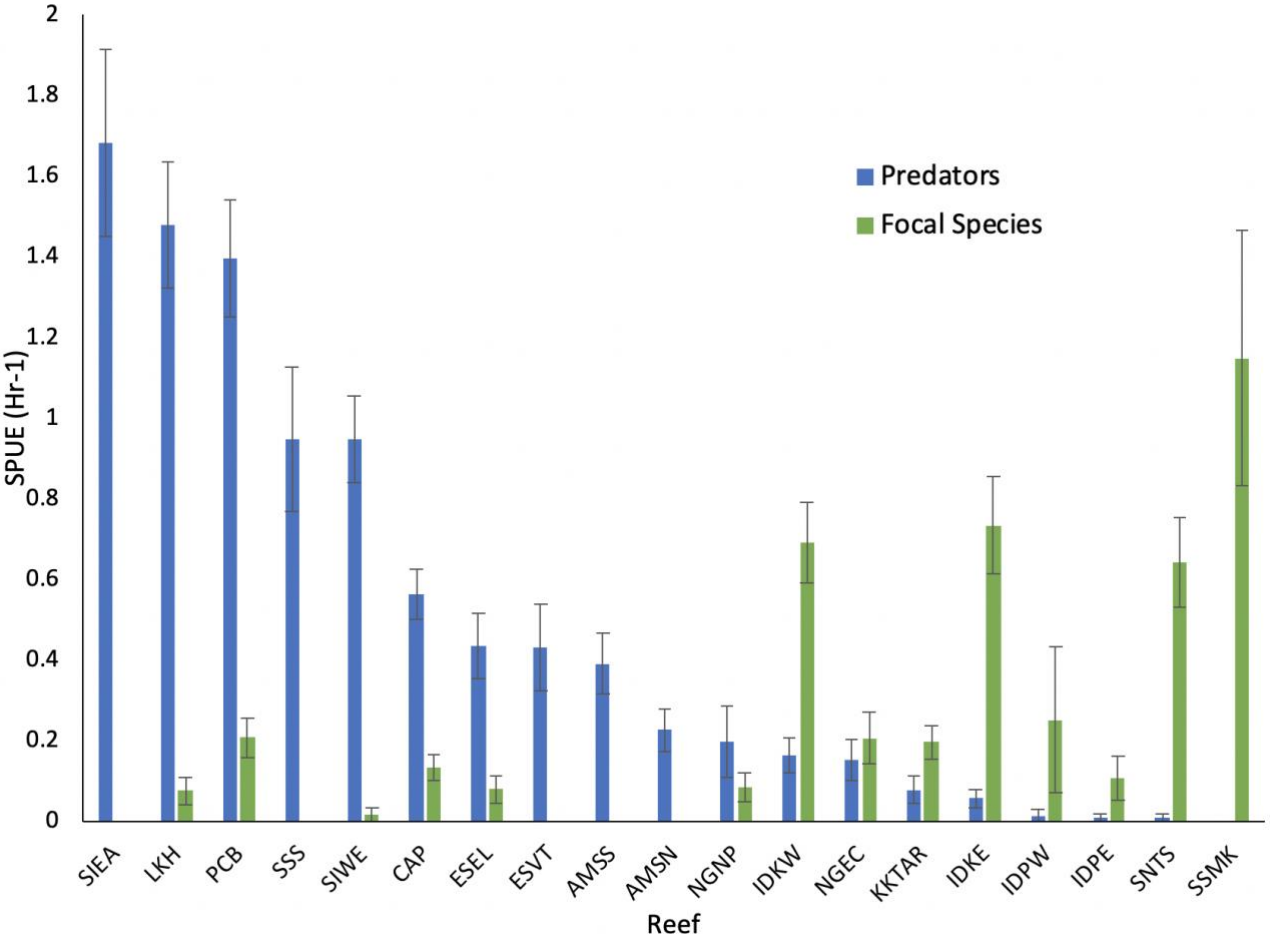


Figure 6.2. Relative abundances of the 19 predator species (SPUE MaxN hr^{-1}) and rays (bluespotted maskray (*Neotrygon* spp.) and fantail rays (*Taeniura* spp.))(MaxIND) across all 19 reefs (+/- SE).

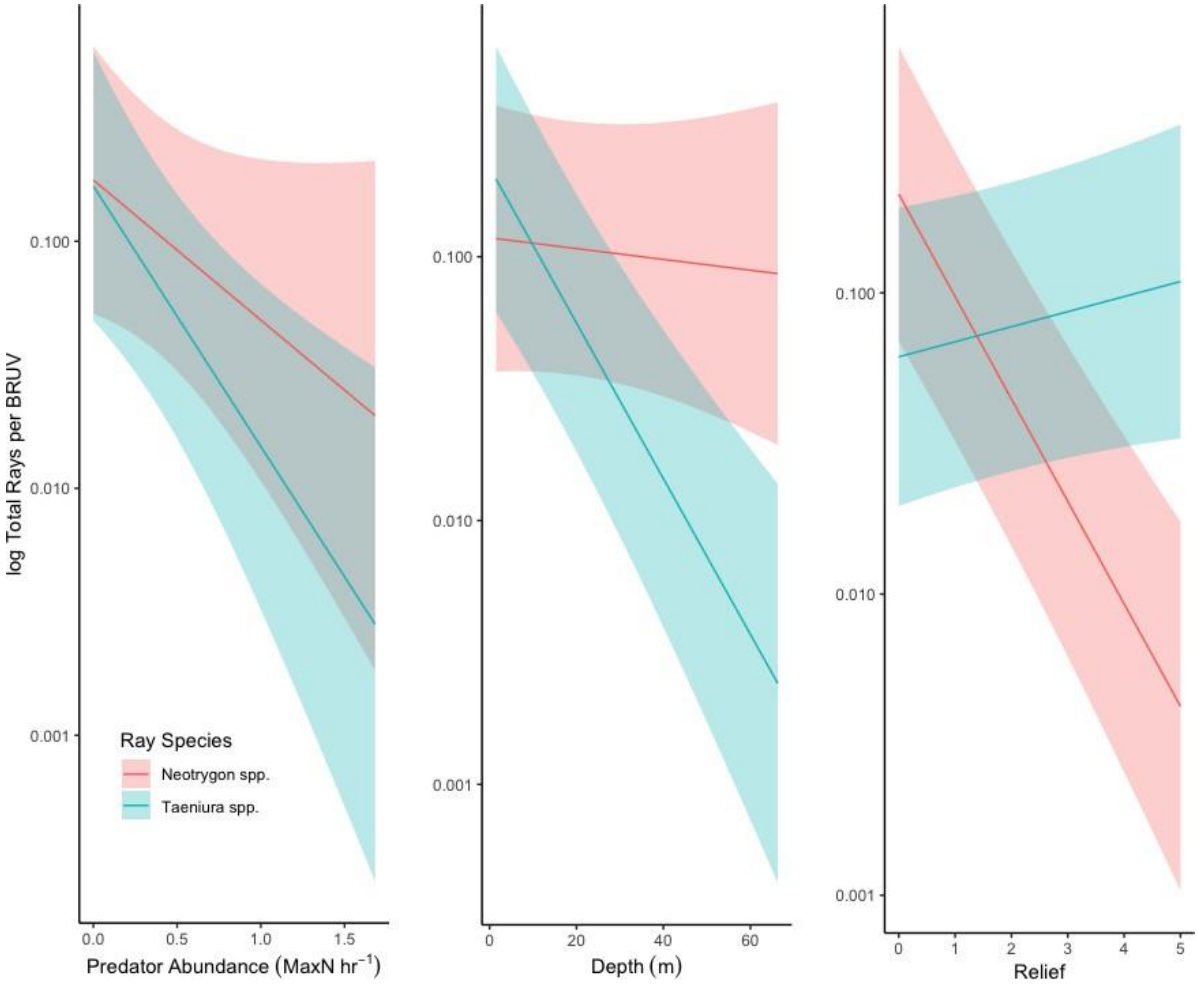
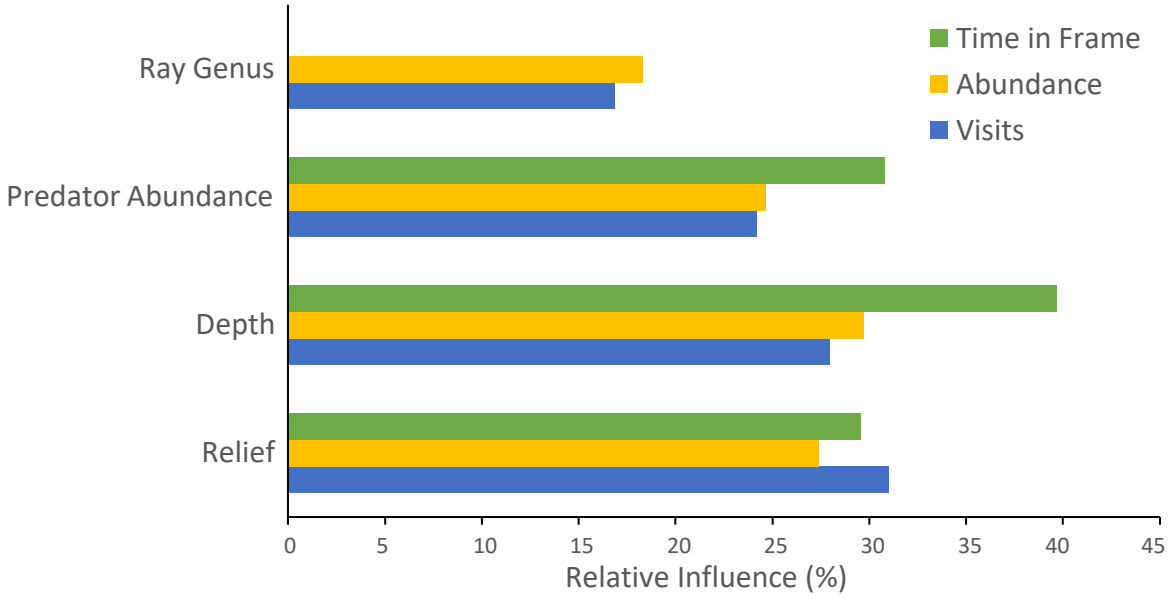


Figure 6.3. Effects of (a) predator abundance, (b) depth, and (c) benthic relief on abundance of *Neotrygon* spp. and *Taeniura* spp. at 19 sites in Southeast Asia and Western Pacific. Lines indicate model predictions and shaded areas are 95% confidence intervals. *Taeniura* spp. were significantly more affected by increasing predator abundance and depth than *Neotrygon* spp., whereas *Neotrygon* spp. sightings were significantly more affected by relief.

A)



B)

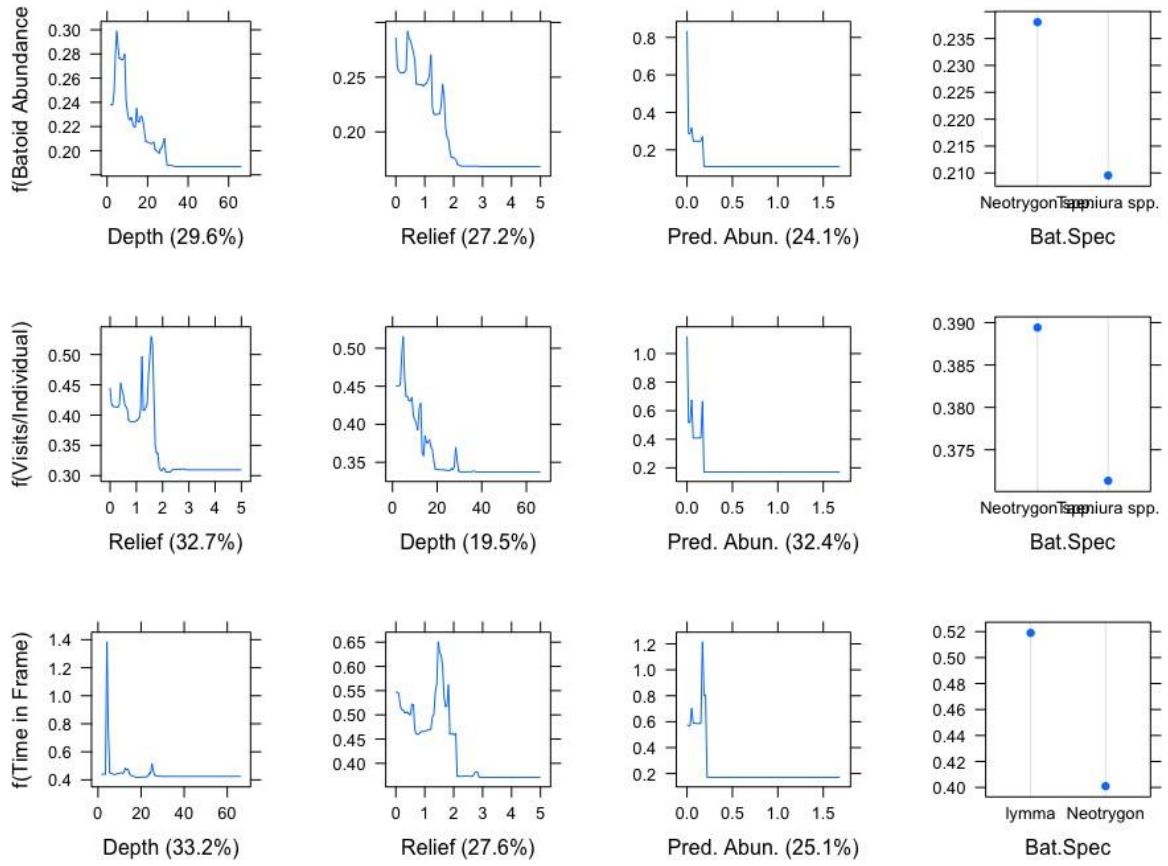


Figure 6.4. A) Relative influences of the explanatory variables for ray abundance, number of visits and proportion of time spent in frame based on generalized boosted regression models (GBM). B) Partial dependence plots from the GBM for ray abundance, number of visits per individual and time spent in frame in descending order of relative importance (listed underneath each plot in parentheses).

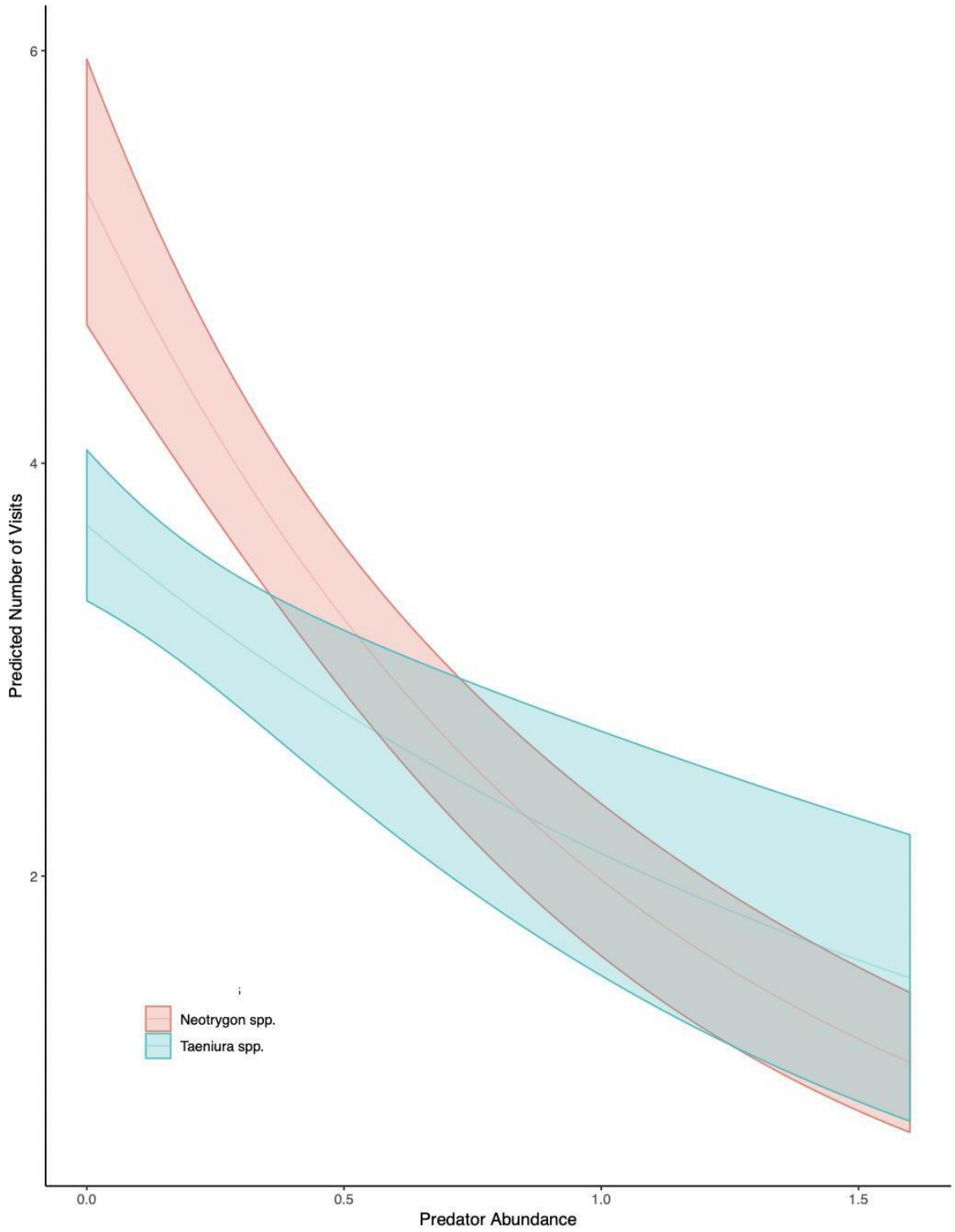


Figure 6.5. Effect of predator abundance on number of visits made by focal species present at 19 sites in Southeast Asia and the Western Pacific. 95% confidence regions are displayed based on a negative binomial generalized linear model.

Table 6.1. Top GLMM models for predicting ray abundance and time in frame, and top hurdle model for predicting number of visits of the focal species. Difference between lowest corrected Akaike Information Criterion (ΔAICc), AIC weights (wAICc), and biggest VIF value of all variables in the model (Biggest VIF) are reported. Model selection was based on the most parsimonious model within two units of the lowest ΔAICc and with the biggest VIF value <5. Selected models are presented in bold. Variable codes: Ray.Gen – ray genus, Pred.Abun – predator abundance, HC – hard coral, UN – unconsolidated, Time – time of day category, CN – consolidated, SC – soft coral, MA – macroalgae, TA – turf algae. For the 'Time in Frame' model, the first model is not selected due to the VIF values being high, therefore, the model with the second smallest AICc value is used.

	Model	ΔAICc	wAICc	Biggest VIF
Abundance (GLMM)	**Ray.Gen*(Pred.Abun + Depth + Relief)**	**0**	**0.81**	**1.03**
	Ray.Gen*(Pred.Abun + Depth + Relief + HC + UN)	2.88	0.19	2.74
	Ray.Gen*(Depth + Relief)	13.51	0	1.03
	Null	111.45	0	-
Visits (hurdle model)	**Ray.Gen*(Pred.Abun + Depth + Relief)**	**0**	**0.43**	**1.03**
	Ray.Gen*(Pred.Abun + Depth + Relief + Tide + Time)	0.26	0.38	1.02
	Ray.Gen*(Pred.Abun + Depth + Relief + HC + UN)	1.66	0.19	2.74
	Null	195.2	0	-
Time in Frame (GLMM)	Pred.Abun + Depth + Relief + HC + UN + CN + SC + MA + TA	0	0.55	40.41
	Pred.Abun + Depth + Relief	**1.98**	**0.20**	**1.03**
	Pred.Abun + Depth + Relief + UN + HC	3.16	0.11	2.84
	Null	43.5	0	-

Chapter 7

General Discussion

Plate 7. Hiking Pulau Siompu in Bau Bau, Indonesia (August 2019).

7.1 Conclusions and Implications

Rays play important roles in marine ecosystems (Suchanek et al. 1986; Ajemian and Powers 2013), however, they are threatened by anthropogenic factors like climate change, fishing, and coastal development (Chin et al. 2010). In order to mitigate the impacts, a thorough understanding of current diversity, abundance, and distribution of rays is necessary. In addition to understanding these attributes, it is important to note how they change with differing levels of human activity and disturbance. Rays are difficult to survey partly due to their cryptic nature (O'Shea et al. 2012a). Recently, baited remote underwater video systems (BRUVS) have proven to be an unbiased survey method for predatory species, including rays (Bernard and Götz 2012). However, there are still some limitations of BRUVS use. This PhD thesis provided new insight into the uses of BRUVS, especially for the surveying of rays. Additionally, a comprehensive description of ray assemblage composition and abundance throughout Southeast Asia and the Western Pacific was provided with explanation of the drivers of patterns observed.

BRUVS have been used to identify assemblage composition and species' abundances most frequently using the metric, MaxN (Whitmarsh et al. 2016). MaxN is the most conservative estimate for abundance as it uses the maximum number of individuals observed in a single frame at a given time to determine abundance. Using this estimate may significantly underestimate abundances of certain species as individuals may enter and exit the frame frequently. In Chapter 3, a new metric, MaxIND, was described to join the range of metrics currently available to researchers. Using MaxIND, identifying all individuals that enter the frame of view, is a more accurate estimate of abundance. In addition to abundance estimates, MaxIND can further be used to determine individual behaviours and even social structure (Haulsee et al. 2016; Towner et al. 2016; Mourier et al. 2017). MaxIND was also

used in Chapter 6 to show rays behaved differently in areas with differing predator abundances. Natural behaviour in wild populations is extremely difficult to study as human presence may influence animal decisions (Williams et al. 2006). The ability to use BRUVS with individual identification allows for behavioural analyses in wild animals (as opposed to a lab setting), in the absence of humans, leading to the behaviours closer to those that are natural being observed. MaxIND does require longer video processing time and the ability to identify individuals from markings, however, to answer specific research questions this timing is justified. In endangered populations, small differences in abundance estimates may have large management implications (McConville et al. 2009). Observing a single individual as opposed to a few individuals could distinguish a rare sighting of a species from an area with high abundances of the species. If refuges are found for endangered species, it would enable these areas to be protected and allow for further research and conservation of the species.

Ray assemblage in different ecosystems is not well known, with only a few studies describing the ray assemblage in an area (Pierce et al. 2011; O'Shea et al. 2012b). Multiple ray species have been documented to have mutualistic relationships. For example, cowtail stingrays (*Pastinachus sephen*) and coach whiprays (*Himantura uarnak*) rest together for faster predator alerts (Semeniuk and Dill 2006). Similarly, pink whiprays (*Pateobatis fai*) have been observed riding on the back of smalleye stingrays (*Dasyatis microps)* and blotched fantail rays (*Taeniurops meyeni*), although the benefits of this are not yet known (Meekan et al. 2016). As shown in Chapter 3, maskrays (*Neotrygon* spp.) had higher population densities than the bluespotted fantail rays (*Taeniura lymma*). This was also observed in Chapter 4, where the maximum MaxN of maskrays observed was nine individuals compared to the maximum MaxN of fantail rays, which was only two individuals.

Living in groups has proven benefits for rays, such as increased protection from predators (Semeniuk and Dill 2006), social learning (Thonhauser et al. 2013), and mating advantages (Kajiura et al. 2000). However, it also increases competition for resources. One reported consequence of competition in ray communities is more injuries from conspecifics (Semeniuk and Rothley 2008). Using BRUVS to estimate true abundances of rays can provide more accurate information on population densities, inter and intraspecific relationships, and space use overlap of individuals and species. This may lead to inferences on species-specific territoriality and overall abundances. There may also be differences to these estimates in areas with varying predator abundances as they may influence ray abundance and behaviour (Chapter 6).

Having accurate abundance estimates of understudied species, like rays, is necessary to understand how fishing pressures may affect populations. Overfishing is the largest threat to rays globally, which are taken in higher abundances than sharks in some areas (Bonfil 1994; Dulvy et al. 2014). Rays are particularly susceptible due to their life history characteristics of slow growth, late maturity, and low fecundity (Simpfendorfer and Wetherbee 2015). Rays can be caught in a variety of fishing methods including: trawl, gill net, hook and line, and long lines (Stobutzki et al. 2002; Uddin et al. 2018). Ease of access by fishermen to fishing grounds plays an important role in the ability to fish, particularly in densely populated, developing countries where rays are fished in high numbers (Dharmadi et al. 2015; Cinner et al. 2018). In developing countries, most coastal fishing is subsistence fishing from small boats that are often not motorized (Asut et al. 2019). Rays are not caught in high numbers from these smaller boats, but when they are rays are kept and sold although they are of limited commercial value (Asut et al. 2019). Other fishing methods, like trawling, have extremely high levels of bycatch and sometimes catch rays in large quantities

(White et al. 2019). Trawling has heavy impacts on the benthic community and is generally performed in lower relief habitats to avoid and reduce gear breakage, which also reduces the disturbance on the sessile benthic community (Collie et al. 2000; Buhl-Mortensen et al. 2016). Coral reef ecosystems are connected through species movement to adjacent habitats in which trawling and other fishing is often prevalent. Understanding the linkages between these trawled areas and coral reefs would enable evaluation of the ability for trawl caught species to have refuge areas on the reefs.

In Chapter 5, it is shown that areas with similar fishing pressures have similar ray communities and abundances. These ray communities were found to be highly conserved throughout the Coral Triangle and Australasian regions, with the exception of Vietnam that was almost devoid of all rays. In heavily fished areas (like Indonesia and Malaysia), rays were abundant but the community was less speciose, being dominated by more productive species like maskrays and fantail rays (Fahmi et al. 2009). These areas also had lower abundances of sharks, as shown in Chapter 6. Ray abundance showed a negative relationship with shark abundance such that with higher shark abundances, rays were less abundant and showed behavioural changes that intensified the perceived differences in abundance. When overfishing occurs, sharks are often the first species to be removed from the environment as they have low productivity and higher value (Myers et al. 2007; Davidson et al. 2016). This removal may lead to mesopredator release, where lower trophic levels, like rays, become more common and thus the dominant predator species (Prugh et al. 2009; Ritchie and Johnson 2009). After an initial increase in ray abundance, with further increases in fishing pressure there may be a threshold reached that then leads to a complete loss of rays (Chapter 5). This reduction can be expedited when the area is fished with gears that have high catch rates for rays, like trawling. Based on these community and

abundance differences, looking at a ray community may enable a measurement of overall reef health and fishing pressure.

BRUVS were used throughout this PhD thesis with a variety of analytical methods. Through identifying individuals and creating a new metric (Chapter 3), it was shown that traditional metrics underestimate abundances. This is generally acknowledged in studies using BRUVS, however, there is now a metric to determine the extent of underestimation. Chapter 3 showed the consistency with which different species abundances were underestimated. This could be extended to other species and taxa, enabling a better understanding of community composition using BRUVS. Similarly, interpreting BRUVS results needs to be completed carefully as other species may be impacting what is observed (Chapter 6). This has also been observed on BRUVS with fish abundance and diversity being lower on videos with sharks (Klages et al. 2014). To get a complete understanding of community composition, other survey methods may need to be used in addition to BRUVS (Boussarie et al. 2018). While there are some drawbacks to using BRUVS, this PhD thesis has also shown they are a repeatable sampling method (Chapter 4). Due to the growing use of BRUVS for ecological studies (Whitmarsh et al. 2016), it is important to understand their consistency. Chapter 4 showed that for rays, BRUVS consistently sampled the population within a season and between years. However, seasonal differences were observed. Many taxa include migratory species and/or species with specific water quality requirements (Maynou et al. 1996; Rosenberg et al. 2004; Pörtner 2010), therefore, comparing results from BRUVS surveys must be completed with care to ensure sampling was performed at a similar time.

This PhD thesis has shown that conservation of rays on coral reefs is dependent on lowering fishing pressure and good capacity for fisheries management. Healthy reefs are those that

have healthy populations of both sharks and rays (Bruno et al. 2014). More work needs to be completed to understand what a healthy ray community looks like on a coral reef. Although rays were more abundant in areas like Indonesia and Malaysia, this may not be accurately reflecting a healthy population. In areas with heavy reliance on marine resources for food, a balance of conservation and food security / income of the human population is required. An understanding of the ecological consequences of higher ray abundance as opposed to higher species richness is necessary in order to ensure reefs with heavy fishing pressure are still healthy. There is some evidence for plasticity in maskray fecundity that may increase the resilience of these rays to overfishing (Fahmi et al. 2009). However, due to the small number of large stingrays observed in areas with high fishing pressure, this plasticity likely does not extend to the larger bodied species of rays. Losing ray diversity in areas with high fishing pressure may mean that important ecological niches are not being occupied, which would negatively impact the overall coral reef ecosystem.

7.2 Future Research Directions

This PhD research provided new insight into the environmental drivers of ray presence on tropical coral reef ecosystems. Having this new, basic data stresses how little information is currently available about rays and the need for more research, particularly on overexploited tropical coral reefs. This thesis highlights the need for species-specific data on biological parameters (growth rate, age at maturity, fecundity, etc.), movement patterns of rays in coral reef ecosystems, and catch in fisheries throughout Southeast Asia and the Australasian regions.

In Chapter 3, a new method (MaxIND) for estimating abundance of rays on BRUVS was developed and tested. MaxIND was only used in this thesis to demonstrate the impact of

identifying individuals. Therefore, rays were only identified within a single deployment, not across deployments. Future research, identifying individuals on BRUVS across all deployments would allow for estimates in population size. Additionally, through repeated sampling, using MaxIND may show residency or movement patterns at a sampling site, or even between sites. Individual identification on BRUVS has already been used to identify a tagged flapper skate (*Dipturus intermedius*)(Benjamins et al. 2018), but there is much more fruitful research that could occur using this approach. Identification on BRUVS can also be used for rare and endangered species, like white sharks (*Carcharadon carcharias*), spotted eagle rays (*Aetobatus narinari*) and manta rays (*Mobula* spp.), and added to existing photo-ID banks which allow for population estimates (Anderson et al. 2011b; Town et al. 2013; González-Ramos et al. 2016).

Chapter 5 showed that in heavily fished countries like Malaysia and Indonesia, small benthic rays were abundant, however, larger rays that occupy a higher trophic level were rare. Two genera of small rays, maskrays (Genus: *Neotrygon*) and fantail rays (Genus: *Taeniura*) comprised the majority of rays observed despite also being caught in large numbers in both commercial and subsistence fisheries. A single study comparing specimens from different regions of Indonesia shows that there is some plasticity in maskray growth and maturity, potentially due to exploitation levels (Fahmi et al. 2009). Further studies into region-specific growth rates and fecundity are important for calculating population growth/decline and to properly measure the impacts of fishing mortality on the local population. Additionally, with increased ray abundances, further work should look at how these abundance changes affect prey species abundances. If rays become too abundant in a region, they may further the trophic cascade started by the reduction in shark abundances and reduce abundances of their prey species (Heupel et al. 2014). This reduction may lead to ecosystem phase shifts as

food availability for mesopredators is reduced (Hughes et al. 2007). Further research should focus on prey species abundances and the sustainability of their populations in regions with high abundances of rays.

As shown in Chapter 4, even in a seemingly consistent environment throughout the year, the abundance of sharks and rays can significantly differ seasonally. This chapter highlights the need for research on movement patterns of both rays and sharks throughout the year. As both rays and sharks were significantly more abundant in the wet season, it is important to understand their movements to ensure the entirety of the area used is well-managed. It remains unknown what environmental aspect of the wet season was driving the differences in observed abundances. Water quality measures (e.g. dissolved oxygen, chlorophyll a, nitrates, temperature, etc.) could be taken at a range of depths throughout the year to determine how these may change on a coral reef (Condie and Dunn 2006) and whether these affect the occurrence of elasmobranchs. Chapter 4 also showed the repeatability of BRUVS sampling within a season, and between years on coral reefs. BRUVS are used in many ecosystems, including rivers, estuaries, and open ocean environments (Lowry et al. 2010; Santana-Garcon et al. 2014; Schmid et al. 2017). Further work should be done to ensure repeatable results can be achieved in these ecosystems as well.

Predator-prey relationships have been studied across many taxa. Chapter 6 adds to the current knowledge of how these interactions may play out in a natural setting. More research should be done to determine the relationship between sharks and larger rays. Anecdotally in the BRUVS used in this thesis, larger rays did not appear to be disturbed by sharks, often appearing together in the video. The larger rays did not leave the frame of view if a shark entered but continued with their activity, seemingly undisturbed. This thesis

is one of the first studies to investigate rays using BRUVS and has shown the need for more in-depth research in species-specific biological parameters that may enable some species to endure high levels of fishing pressure. The implications of this thesis also establish the need for more detailed catch records to understand species presence throughout Southeast Asia and the Australasian regions. Currently, ray catch data is often grouped as “rays” and there is a lack of species-specific data. Having an idea of the complete ray assemblage within the region would allow for a better understanding of species at risk and species of economic importance. Once these species-specific attributes are known, future management could be put in place to conserve at-risk species and ensure there are sustainable levels of fishing for species of economic importance.

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APPENDICES

Appendix I Reef information for the 70 reefs included in this study. Number of individual deployments, geographical range of the deployments, and the time of sampling are included.

Country	Site	Site Code	Reef	Reef Code	Number of Deployments	Latitudinal Range	Longitudinal Range	Month/Year Sampled
Australia - Indian	Ashmore	ASH	Ashmore East	ASAE	51	-12.286116 to -12.17276	123.062235 to 123.216177	Jan-16
Australia - Indian	Ashmore	ASH	Ashmore West	ASAW	46	-12.301347 to -12.171144	122.913474 to 123.05812	Jan-16
Australia - Pacific	Central GBR	CGB	Chicken Reef	TSV3	47	-18.671988 to -18.650339	147.701329 to 147.724531	Jan-16
Australia - Pacific	Central GBR	CGB	Helix Reef	TSV2	15	-18.629932 to -18.618754	147.292358 to 147.30027	Jan-16
Australia - Pacific	Central GBR	CGB	Knife Reef	TSV4	51	-18.592449 to -18.568356	147.561332 to 147.58153	Jan-16
Australia - Pacific	Central GBR	CGB	Rib Reef	TSV1	52	-18.493809 to -18.467008	146.859956 to 146.886826	Jan-16
Australia - Indian	Cobourg Peninsula	COP	Airport Beach	CPAB	60	-11.1633 to -11.0459	132.074997 to 132.197006	Dec-16
Australia - Indian	Cobourg Peninsula	COP	Offshore Reef	CPOR	16	-11.1632 to -11.1394	132.220001 to 132.231995	Dec-16
Australia - Pacific	Northern GBR	NGB	13-124	PCB2	41	-13.895429 to -13.68659	144.00507 to 144.66775	Nov-15
Australia - Pacific	Northern GBR	NGB	Corbett Reef	PCBC	51	-13.99641 to -13.88025	144.18689 to 144.2438	Nov-15
Australia - Pacific	Northern GBR	NGB	Lagoon Reef	LKHL	30	-12.401552 to -12.22174	143.45488 to 143.784785	Nov-15

Australia - Pacific	Northern GBR	NGB	Mantis Reef	LKHM	30	-12.3346 to -12.232	143.3089 to 143.9231	Nov-15
Australia - Indian	Rowley Shoals	ROS	Clerke Reef	RSCR	41	-17.3971 to -17.24798	119.35536 to 119.38516	Sep-16
Australia - Indian	Rowley Shoals	ROS	Imperieuse Reef	RSIR	18	-17.62653 to -17.54303	118.96609 to 118.97861	Sep-16
Australia - Indian	Scott Reef	SCR	North	SRNO	50	-13.96779 to -13.87519	121.85763 to 121.94838	Sep-16
Australia - Indian	Scott Reef	SCR	South	SRSO	48	-14.17009 to -14.06208	121.91909 to 121.98128	Sep-16
Australia - Pacific	Southern GBR	SGB	Heron/Wistari Green	SHWG	52	-23.488303 to -23.432192	151.885183 to 151.981816	Apr/May-16
Australia - Pacific	Southern GBR	SGB	Heron/Wistari Yellow	SHWY	55	-23.492791 to -23.425413	151.829619 to 152.00591	Apr/May-16
Australia - Pacific	Southern GBR	SGB	One Tree Island	SHOT	19	-23.50713 to -23.47791	152.0408 to 152.10051	Jun-18
Indonesia	Bau Bau	BAU	Coast	BBCO	74	-5.66777 to -5.4282	122.53928 to 122.61642	Mar-17
Indonesia	Bau Bau	BAU	Islands	BBIL	90	-5.64851 to -5.2776	122.466993 to 122.5571	Mar-17
Indonesia	Kopoposang	KOP	Open	KOOP	178	-4.8573 to -4.5538	118.918267 to 119.18825	Apr-16
Indonesia	Kopoposang	KOP	Protected	KOPA	12	-4.717967 to -4.643283	118.93405 to 119.13235	Apr-16
Indonesia	North Sulawesi	NSW	Bangka Island	NSWB	82	1.083017 to 1.88661	125.03878 to 125.18856	Jul-16
Indonesia	North Sulawesi	NSW	Lembeh Island	NSWL	63	1.4555 to 1.59734	125.15685 to 125.29659	Jul/Aug-16
Indonesia	North Sumatra	NSM	Aceh Closed	NSMA	53	5.52309 to 5.75402	95.03218 to 95.19363	Aug-16
Indonesia	North Sumatra	NSM	Weh Closed	NSMC	23	5.83338 to 5.90537	95.31179 to 95.37831	Aug-16

Indonesia	North Sumatra	NSM	Weh Open	NSMO	35	5.84092 to 5.90522	95.22608 to 95.30378	Aug-16
Indonesia	Nusa Penida	NUP	East	NPEA	57	-8.819933 to -8.689333	115.509383 to 115.629083	Mar-16
Indonesia	Nusa Penida	NUP	West	NPWE	59	-8.77205 to -8.659783	115.429033 to 115.57095	Mar-16
Japan	Okinawa	OKI	Iriomote	OKIR	53	24.24116 to 24.40701	123.86411 to 124.00317	May-17
Japan	Okinawa	OKI	Kuroshima	OKKU	53	24.21217 to 24.27999	123.90934 to 124.03759	May-17
Malaysia	Kota Kinabalu	KOK	Tunku Abdul Rahman Park	KKTA	97	5.946533 to 6.08645	115.986467 to 116.092667	Dec-15
Malaysia	Kuala Terrenganu	KUT	Pulau Redang	KTPR	53	5.72825 to 5.8187	102.888633 to 103.059067	Mar-17
Malaysia	Perhentian	PER	West	PNWE	47	5.88165 to 5.960767	102.654783 to 102.768217	Mar-17
Malaysia	Semporna North	SEN	Tun Sakaran Marine Park	SNTS	96	4.5723667 to 4.6860167	118.639217 to 118.808233	Dec-15
Malaysia	Semporna South	SES	Mabul / Kapalai	SSMK	66	4.202267 to 4.262967	118.606767 to 118.699267	Dec-15
Malaysia	Semporna South	SES	Sipadan	SSSI	21	4.1029667 to 4.1230667	118.624883 to 118.636617	Dec-15
Malaysia	Tioman	TIO	East	TIEA	56	2.1346833 to 2.8973833	104.028167 to 104.224783	Feb-17
Malaysia	Tioman	TIO	West	TIWE	52	2.66105 to 2.93355	104.049467 to 104.168983	Feb-17
Papua New Guinea	Conflict Islands	COI	Milne Bay Lagoon	CIML	52	-10.81942 to -10.72474	151.71204 to 151.9115	Oct-17
Papua New Guinea	Conflict Islands	COI	Outer Milne	CIMO	50	-10.82415 to -10.67555	151.63196 to 151.91481	Oct-17
Papua New Guinea	Kavieng	KAV	Kapalaman	KVKP	51	-2.61676 to -2.55054	150.78853 to 150.88562	Sep-17

Papua New Guinea	Kavieng	KAV	Tsoi Island	KVTS	47	-2.45245 to -2.39148	150.39616 to 150.48932	Sep-17
Papua New Guinea	Kimbe Bay	KMB	Hoskins Lagoon	KBHL	51	-5.97252 to -5.33491	150.34917 to 150.3979	Oct-17
Papua New Guinea	Kimbe Bay	KMB	Restoff Island	KBRI	50	-5.4544 to -5.29343	150.05818 to 150.11024	Oct-17
Philippines	Cagayan Island	CAG	Cagayancillo	CGCG	42	9.584889 to 10.021667	121.248611 to 121.55333	May/Jun-16
Philippines	Cagayan Island	CAG	Cawili	CGCW	14	9.303333 to 9.542222	120.80944 to 121.09222	May-16
Philippines	Luzon	LUZ	Matnog	LZMA	44	12.519887 to 12.692602	124.030835 to 124.141121	Mar-16
Philippines	Mindoro	MIN	Apo Reef	MIAP	35	12.638399 to 12.724939	120.407997 to 120.530117	Jan/Feb-16
Philippines	Mindoro	MIN	Sablayan Closed	MISA	21	12.67856 to 12.859884	120.659688 to 120.786083	Feb-16
Philippines	Oslob	OSL	Cabilao	OSCB	39	9.51695 to 9.53587	123.45492 to 123.47598	Nov-16
Philippines	Sulu	SUL	Tubbataha	SUTU	88	8.44334 to 9.0296	119.48667 to 120.093056	Apr-Jun-16
Solomon Islands	Gizo Area	GIZ	Open	GIOP	66	-8.2002356 to -8.0271174	156.886625 to 157.060175	Oct-15
Solomon Islands	Zaira Area	ZAI	Open	ZAOP	30	-8.8031703 to -8.7552105	157.933743 to 158.319005	Oct-15
Solomon Islands	Zaira Area	ZAI	Protected	ZAPA	10	-8.8065096 to -8.7904669	157.964127 to 158.004077	Oct-15
Taiwan	Dongsha	DON	Lagoon	DOLA	51	20.642278 to 20.744869	116.695977 to 116.807641	Apr-17
Taiwan	Dongsha	DON	Outer	DOOU	35	20.591894 to 20.752277	116.69224 to 116.769441	Apr-17
Taiwan	Green Island	GRI	Green Island	GIGI	42	22.632017 to 22.691292	121.461244 to 121.51907	Mar-17

Taiwan	Orchid Island	ORI	Orchid Island	OIOI	51	21.94213 to 22.088817	121.497933 to 121.618889	Mar-17
Taiwan	Penghu	PEN	Cimei	PECI	49	23.188363 to 23.289645	119.41422 to 119.666398	Apr-17
Taiwan	Penghu	PEN	North	PENO	54	23.242815 to 23.413123	119.310418 to 119.671271	Apr-17
Vanuatu	Espiritu Santo	ESS	East Luganville	ESEL	55	-15.59352 to -15.40618	167.23512 to 167.29955	Oct-16
Vanuatu	Espiritu Santo	ESS	Vuti	ESVT	53	-15.64138 to -15.5825	166.89778 to 167.07216	Oct-16
Vanuatu	Nguna	NGU	Emao / Coast	NGEC	51	-17.59712 to -17.46551	168.45099 to 168.511	Sep-16
Vanuatu	Nguna	NGU	Nguna / Pele	NGNP	52	-17.50657 to -17.41027	168.31938 to 168.42674	Sep-16
Vietnam	Con Dao Islands	CDI	Con Dao	CDCD	49	8.63933 to 8.71245	106.53608 to 106.70924	Oct-17
Vietnam	Ninh Thuan	NIT	North	NTNT	34	11.7136 to 11.81451	109.195 to 109.23319	Jul-17
Vietnam	Ninh Thuan	NIT	South	NTST	36	11.51456 to 11.71209	109.13106 to 109.2027	Jul-17
Vietnam	Phu Quoc	PHQ	An Thoi	PQAT	31	9.90721 to 10.01236	103.9849 to 104.04244	Nov-17

Appendix II ANOSIM and SIMPER results for differences in ray abundances at each country. Boxes below the diagonal represent results of ANOSIM. Countries with significantly different assemblages are shaded with bolded numbers. R – R-statistic, P – P-value, N- Permutations completed. Diagonal line is result of SIMPER analysis looking at similarity in assemblages within different reefs in each country. The top number within each box is the percent similarity and species responsible for similarities are listed below. Boxes above the diagonal indicate SIMPER results of dissimilarity between countries. Dissimilarity percentage is reported followed by species responsible for differences. MSK – Maskrays, EAG – Eagle rays, FAN – Fantail rays, PIN – Pink whipray, DEV – Devil / Manta rays, BLO – Blotched fantail ray, and MNG – Mangrove whipray. Headers represent country codes: AUI – Australia (Indian Ocean), AUP – Australia (Pacific Ocean), IDN – Indonesia, JPN – Japan, MYS – Malaysia, PNG – Papua New Guinea, PHL – Philippines, SLB – Solomon Islands, TWN – Taiwan, VUT – Vanuatu, and VNM – Vietnam.

	AUI	AUP	IDN	JPN	MYS	PNG	PHL	SLB	TWN	VUT	VNM
AUI	17.14 EAG - 57.29 PIN - 20.05	79.72 MSK – 25.53 EAG – 17.56 FAN – 16.25	81.70 FAN - 26.01 MSK - 21.82 EAG - 13.91	76.06 MSK - 34.72 EAG - 15.97 PIN – 8.76	80.75 FAN - 27.85 EAG – 18.51 MSK - 17.37	71.70 MSK - 21.18 FAN – 19.66 EAG - 16.35	75.89 EAG - 33.53 PIN - 15.48 MSK - 11.40	88.95 EAG – 40.38 PIN - 15.18 MNG - 12.58	87.44 EAG – 21.55 MSK - 16.41 PIN - 16.41	71.35 MSK - 25.28 EAG - 24.97 FAN - 10.39	92.36 EAG - 40.29 PIN - 17.19 MNG - 11.16
AUP	**R = 0.251** **P = 0.005** **N = 999**	43.14 MSK - 62.45 EAG – 16.95	58.82 FAN – 26.85 MSK – 17.83 EAG – 15.76	52.05 MSK - 24.44 FAN - 18.92 EAG - 15.57	63.11 FAN - 28.62 MSK - 26.11 EAG - 14.84	50.61 FAN – 19.69 MSK - 17.67 EAG - 17.36	79.17 MSK - 34.94 FAN - 21.09 EAG - 16.43	90.88 MSK - 35.72 EAG - 21.39 FAN - 21.23	76.56 MSK - 24.56 FAN - 17.78 EAG - 15.33	52.77 MSK - 26.51 EAG - 23.18 FAN - 20.17	95.30 MSK - 39.58 FAN - 23.68 EAG - 16.39
IDN	**R = 0.226** **P = 0.016** **N = 999**	**R = 0.122** **P = 0.018** **N = 999**	45.44 FAN - 40.18 MSK - 39.34	62.55 FAN - 30.38 MSK - 17.57 EAG - 14.45	60.27 FAN - 23.83 MSK - 23.76 EAG - 14.97	50.11 FAN - 20.28 MSK - 18.57 EAG - 17.61	86.95 FAN - 30.79 MSK - 26.64 EAG - 13.63	89.91 FAN - 29.13 MSK - 28.30 EAG - 15.56	80.55 FAN - 27.77 MSK - 21.28 EAG - 12.93	60.39 FAN - 27.01 MSK - 21.08 EAG - 18.11	97.54 FAN - 32.25 MSK - 29.29 EAG - 12.74
JPN	R = 0.043 P = 0.378 N = 45	R = -0.090 P = 0.615 N = 78	R = -0.130 P = 0.667 N = 78	48.20 MSK - 63.40 EAG - 36.60	67.33 FAN - 28.23 MSK - 28.08 EAG - 12.93	51.02 FAN - 24.65 MSK - 20.85 DEV - 11.47	66.35 MSK - 53.40 DEV - 11.95 BLO - 11.95	92.05 MSK - 43.27 EAG - 24.49 DEV - 9.40	74.31 MSK - 32.52 EAG - 21.13 BLO - 11.33	42.20 MSK - 37.43 FAN - 15.05 DEV - 12.38 BLO - 12.38	92.35 MSK - 49.66 EAG - 20.53
MYS	**R = 0.181** **P = 0.014** **N = 999**	**R = 0.158** **P = 0.043** **N = 999**	R = -0.055 P = 0.756 N = 999	R = 0.147 P = 0.178 N = 45	35.62 FAN - 54.93 MSK - 20.70	54.67 MSK - 23.99 FAN - 20.99 EAG - 16.64	83.65 FAN - 34.27 EAG - 20.81 MSK - 20.43	89.18 FAN - 34.09 EAG - 22.11 MSK - 20.38	84.66 FAN - 27.99 MSK - 20.59 EAG - 12.94	60.62 FAN - 27.98 MSK - 26.54 EAG - 21.07	96.02 FAN - 38.52 MSK - 21.43 EAG - 18.80
PNG	**R = 0.221** **P = 0.030** **N = 999**	R = 0.033 P = 0.379 N = 999	R = -0.110 P = 0.861 N = 999	R = 0.125 P = 0.357 N = 28	R = 0.051 P = 0.253 N = 999	59.34 FAN - 31.89 MSK - 30.53 EAG - 27.82	73.22 MSK - 27.45 FAN - 26.21 EAG - 12.19	85.66 MSK - 26.26 EAG - 23.71 FAN - 20.55	75.45 EAG - 20.54 FAN - 19.55 MSK - 17.93	45.25 MSK - 25.45 FAN - 17.80 PIN - 13.28	93.69 MSK - 27.19 EAG - 24.70 FAN - 20.19
PHL	R = 0.023 P = 0.225 N = 999	**R = 0.239** **P = 0.025** **N = 999**	**R = 0.234** **P = 0.017** **N = 999**	**R = 0.860** **P = 0.028** **N = 36**	**R = 0.295** **P = 0.011** **N = 999**	**R = 0.652** **P = 0.001** **N = 999**	41.94 EAG - 100	90.97 EAG - 64.80 MSK - 6.76	90.39 EAG - 26.29 MSK - 20.89 BLO - 17.79	64.38 MSK - 36.84 EAG - 26.77 FAN - 15.17	81.64 EAG - 67.90 MSK - 9.16

SLB	R = -0.185 P = 0.782 N = 165	R = 0.296 P = 0.069 N = 364	R = 0.050 P = 0.332 N = 364	**R = 0.333** **P = 0.020** **N = 10**	R = 0.074 P = 0.267 N = 165	**R = 0.395** **P = 0.024** **N = 84**	R = 0.190 P = 0.158 N = 120	0.00 None	96.56 MSK - 24.90 BLO - 21.07 EAG - 17.58	84.14 EAG - 44.60 MSK - 30.24	94.95 EAG - 75.90
TWN	R = -0.031 P = 0.0.546 N = 999	R = 0.169 P = 0.084 N = 999	R = 0.121 P = 0.132 N = 999	R = 0.229 P = 0.250 N = 28	R = 0.164 P = 0.076 N = 999	**R = 0.429** **P = 0.006** **N = 462**	**R = 0.239** **P = 0.009** **N = 999**	R = -0.043 P = 0.452 N = 84	15.17 MSK - 56.32 BLO - 31.29	78.67 EAG - 31.02 MSK - 24.36 BLO - 11.47	99.03 MSK - 29.26 BLO - 24.51 PIN - 15.93
VUT	R = 0.003 P = 0.426 N = 495	R = -0.194 P = 0.922 N = 999	R = -0.126 P = 0.725 N = 999	R = -0.107 P = 0.600 N = 15	R = 0.017 P = 0.364 N = 495	R = -0.103 P = 0.752 N = 210	**R = 0.552** **P = 0.015** **N = 330**	R = 0.315 P = 0.143 N = 35	**R = 0.302** **P = 0.048** **N = 210**	56.96 EAG - 57.87 MSK - 28.09	90.20 EAG - 43.72 MSK - 32.37
VNM	R = -0.141 P = 0.828 N = 495	R = 0.173 P = 0.144 N = 999	R = 0.083 P = 0.259 N = 999	R = 0.857 P = 0.067 N = 15	R = 0.082 P = 0.202 N = 495	**R = 0.528** **P = 0.019** **N = 210**	R = -0.034 P = 0.624 N = 330	R = 0.000 P = 0.429 N = 35	R = -0.048 P = 0.533 N = 210	**R = 0.656** **P = 0.029** **N = 35**	0.00 None

Appendix III Locations and number of BRUVS deployed for each reef (Chapter 6).

Country	Reef	Site Code	Latitude Range	Longitude Range	Number of BRUVS Deployed
American Samoa	North	AMSN	-14.32707 to -14.24669	-170.84275 to -170.58318	58
American Samoa	South	AMSS	-14.36816 to -14.27510	-170.84752 to -170.57478	49
Australia	Heron Island	CAP	-23.49279 to -23.42541	151.82962 to 152.00591	111
Australia	Lockhart Reef	LKH	-12.40155 to -12.23385	143.74141 to 143.92247	60
Australia	Princess Charlotte Bay	PCB	-13.82859 to -13.93717	144.06080 to 144.24265	89
Indonesia	East	IDKE	-4.85730 to -4.55380	119.06031 to 119.18825	91
Indonesia	West	IDKW	-4.85730 to -4.55380	118.91827 to 119.06031	86
Indonesia	East	IDPE	-8.81993 to -8.68933	115.50938 to 115.62908	57
Indonesia	West	IDPW	-8.77205 to -8.65978	115.42630 to 115.57095	59
Malaysia	Tunku Abdul Rahman Park	KKTAR	5.79222 to 6.08645	115.98647 to 116.09267	97
Malaysia	Tun Sakaran Marine Park	SNTS	4.57237 to 4.68602	118.63922 to 118.80823	96
Malaysia	Mabul / Kapalai	SSMK	4.20227 to 4.26297	118.60677 to 118.69927	66
Malaysia	Sipadan	SSS	4.10297 to 4.12307	118.62488 to 118.63662	21

Solomon Islands	East	SIEA	-8.80651 to -8.75521	157.93374 to 158.31901	40
Solomon Islands	West	SIWE	-8.20024 to -8.02712	156.88663 to 157.06018	66
Vanuatu	East Luganville	ESEL	-15.59352 to -15.40618	167.20082 to 167.29955	55
Vanuatu	Vuti	ESVT	-16.54113 to -15.55035	166.89778 to 167.15190	53
Vanuatu	Nguna / Pele	NGNP	-17.54558 to -17.41027	168.31938 to 168.42674	52
Vanuatu	Emao / Coast	NGEC	-17.59712 to -17.46551	168.43019 to 168.51100	51

Appendix IV Elasmobranch species included in predator abundance.

- Blacktip reef shark (*Carcharhinus melanopterus*)
- Bull shark (*Carcharhinus leucas*)
- Common blacktip shark (*Carcharhinus limbatus/tilstoni*)
- Fossil shark (*Hemipristis elongata*)
- Great hammerhead (*Sphyrna mokarran*)
- Grey reef shark (*Carcharhinus amblyrhynchos*)
- Hardnose shark (*Carcharhinus macloti*)
- Lemon shark (*Negaprion acutidens*)
- Nurse shark (*Nebrius ferrugineus*)
- Sandbar shark (*Carcharhinus plumbeus*)
- Scalloped hammerhead (*Sphyrna lewini*)
- Silvertip shark (*Carcharhinus albimarginatus*)
- Spottail shark (*Carcharhinus sorrah*)
- Thresher shark (*Alopias* spp.)
- Tiger shark (*Galeocerdo cuvier*)
- Wedgefish (*Rhynchobatus* spp.)
- Whitecheek shark (*Carcharhinus dussumieri*)
- Whitetip reef shark (*Triaenodon obesus*)
- Wobbegong (*Orectolobus* spp.)